CHEATGRASS – NATIVE PLANT COMMUNITY INTERACTIONS IN AN INVADED SOUTHWESTERN FOREST

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ABSTRACT

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Invasions by nonnative plant species such as cheatgrass (*Bromus tectorum*) are a major concern in many ecosystems worldwide. When invasive nonnative species dominate a new ecosystem, they can alter biodiversity, species composition, nutrient cycles, disturbance regimes, and other ecosystem functions and processes. In 2003, cheatgrass rapidly spread through the Mt. Trumbull Ecosystem Restoration Project in the Uinkaret Mountains of northwest Arizona. In several areas, cheatgrass became the dominant herbaceous species, although native vegetation continued to dominate a substantial portion of the landscape. The three studies I present here examine the roles of disturbance, propagule pressure, competition, and resource availability on cheatgrass – native plant dynamics. The first study examines the susceptibility of remnant native vegetation to cheatgrass invasion, and persistence of the cheatgrass invasion in the presence of elevated disturbance through biomass removal and/or elevated propagule pressure through seed additions. Both cheatgrass- and native-dominated areas were persistent for three years after treatment. The second study monitored changes in plant species richness, composition, and distribution in invaded and non-invaded areas. The two community types only shared 52 – 59% of plant species one year after invasion. By the fifth year, the invaded and non-invaded areas only shared 32 – 41% of plant species. Furthermore, the invaded plots contained more nonnative species than the uninvaded plots. By 2007, nonnative species accounted for 30% of species richness in the invaded

community. The third study was a greenhouse experiment testing cheatgrass competition against two native perennial grass species at different levels of competition, with nitrogen and phosphorus additions, and at high and low water availability. Competition with only a single mature perennial grass individual significantly reduced cheatgrass growth and seed production regardless of nutrient and water availability. The greenhouse results, combined with the field studies suggest that the maintenance of a robust native perennial grass community can be important in a plant community's ability to resist invasion by nonnative annual grass species.

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Table of Contents

List of Tables

List of Figures

PREFACE

The first chapter of this dissertation is a literature review. The last three chapters were written in journal manuscript format. Since they are intended for publication with co-authors, I have retained the third person pronouns throughout those chapters. Additionally, there was unavoidable redundancy in the chapters, particularly in the Methods and Reference sections. The second chapter is currently in review with *Biological Invasions*, the third chapter is formatted for submission to *Plant Ecology*, and the fourth chapter is formatted for submission to *Journal of Ecology*.

Chapter 1
The role of soil nitrogen and phosphorus in arid and semi-arid ecosystems invaded by nonnative plant species

Abstract

As nonnative plant species invade more arid and semi-arid landscapes, there is increasing interest in the interaction of soil nutrients and plant invasions. Soil nitrogen (N) and phosphorus (P) are often the most limiting soil nutrients in arid and semi-arid ecosystems. The differential ability of native and nonnative species to exploit these nutrients influences spatial and temporal patterns of plant invasion. I reviewed the role of soil N and P in invasion dynamics, the influence of plant invasions on soil N and P, and the utility of altering soil N and P to mitigate nonnative species dominance in invaded ecosystems. Many invasive nonnative plant species preferentially invade areas with high levels of plant-available N. This relationship can be enhanced by fire, which generates pulses of plant-available soil N and disturbs the extant vegetation. Less is known about the role of plant-available soil P and invasion success. After invasion, plants can influence soil N dynamics by altering fire regimes, soil biota, or by depleting resources. Post-invasion soil P dynamics are complex. Some nonnative plants can alter the availability of soil P through input of acidic compounds via root exudation or aboveground biomass leachates that liberate calcium-bound P. Furthermore, some nonnative plants have been shown to deplete soil P through rapid uptake. Manipulation of the link between invasion success and available N and P may provide a mechanism for mitigating nonnative plant invasions. Most research on this topic has been on soil N manipulation through carbon additions such as sucrose or sawdust. Plant-available P can also be altered through calcium additions to the soil. To date, however, successful

invasion reduction through soil nutrient manipulation has proven either impractical or ineffective.

Introduction

Nonnative plant invasions are a major global concern. Plant invasions can result in the loss or alteration of biodiversity, changes in disturbance regimes such as the fire cycle, and changes in ecosystem processes such as soil hydrology and nutrient cycling (Bock et al. 1986; Melgoza et al. 1990; D'Antonio and Vitousek 1992; Hobbs and Huenneke 1992; Mack et al. 2000; Belnap and Phillips 2001; Evans et al. 2001; Ehrenfeld 2003; Brooks et al. 2004; Gerlach Jr. 2004; Gurevitch and Padilla 2004; Kulmatiski et al. 2006). Such changes are evident in invaded areas of arid and semi-arid ecosystems of the western United States. A number of annual nonnative plant species that invade arid and semi-arid ecosystems of the West are highly dependent on high availability of soil nutrients, especially nitrogen (N) and phosphorus (P) (Marschner 1995). There is also evidence that some longer-lived nonnative species thrive in high nutrient sites as well (Floyd et al. 2006; Miller and Seastedt 2009). N and P are considered to be the most commonly limiting nutrients for plant productivity in many ecosystems worldwide (Elser et al. 2007), including the drier regions of the West. This has generated increasing interest in the role of soil N and P interactions with nonnative plant invasions with regards to ecosystem invasibility, post-invasion ecosystem change, and remediation of invasions. The purpose of this review is to synthesize published research on the relationship between plant-available N and P and nonnative plants in arid and semi-arid ecosystems of the western United States and to evaluate how such knowledge can be incorporated into management strategies for invaded areas.

There is evidence that success and spatial distribution of a number of plant invasions in the West are often influenced by the quantity and distribution of plant-

available N and P. Nonnative plants commonly invade areas with higher soil nutrients, particularly if nutrient availability is elevated due to disturbances such as fire or cattle grazing (Hobbs and Huenneke 1992). Many annual nonnative plants are better competitors for soil nutrients than native annuals or perennial seedlings. Conversely, perennial species, particularly grasses, are more efficient at extracting and conserving N and P on nutrient-poor soils (Grime 1977; Chapin 1980).

Once a nonnative species dominates a plant community, cycling and plant availability of N and P are often altered (Trent et al. 1994; Vinton and Burke 1995; Evans et al. 2001; Hawkes et al. 2005; Sperry et al. 2006). Several mechanisms contribute to the changes in post-invasion nutrient availability, including changes in soil moisture, C:N ratio, fire frequency and intensity, soil biota, and root exudates (Booth et al. 2003a; Belnap et al. 2005; Saetre and Stark 2005; Belnap and Sherrod 2009). There is evidence that post-invasion changes in soil N and P can help perpetuate nonnative plant dominance by maintaining a competitive advantage for nonnative plants.

The close link between nonnative plants and soil nutrients has encouraged ecologists to test the utility of altering soil nutrients in order to reduce nonnative plant dominance in invaded ecosystems. Nitrogen is the most frequently targeted nutrient, with carbon amendments to the soil being the most common treatment (Beckstead and Augspurger 2004; Keeley and McGinnis 2007). Carbon amendments stimulate soil microbial activity, which in turn binds pools of plant available N in microbial biomass. Some studies have also examined the utility of reducing P availability in the soil through chemical amendments such as calcium oxide (Belnap et al. 2003; Keeley and McGinnis 2007).

I reviewed 69 articles that addressed the interaction of soil N and P and nonnative plant invasions. I focused on information from arid and semi-arid regions of the Interior West of the United States. The review mostly focuses on deserts and grasslands, but includes examples from other non-riparian woodland and low-elevation forests. I examined the literature over the past 100 years, but when several studies reported similar results, I focused on the most recent studies.

The role of N and P in invasion dynamics

There is rarely information available regarding soil nutrients at the time of invasion. Furthermore, researchers are, understandably, disinclined to induce large-scale plant invasions to test hypotheses about soil nutrient-invasion dynamics. Most information on this topic, therefore, comes from comparing neighboring invaded and non-invaded areas or from soil nutrient manipulations made after invasion or in greenhouse studies. While these methods are far from perfect, they do give insight about the role of soil N and P in constraining or promoting invasion.

Nitrogen

High levels of plant-available nutrients are often associated with increased risk of invasion, while low fertility soils can be resistant to invasion. A good example of resistance to invasion is serpentine soil in California grasslands. Serpentine soils are created from tectonically derived rock and tend to have low N and P availability (Huenneke et al. 1990). While serpentine soils have shown little susceptibility to invasion, many neighboring areas of fertile nonserpentine soils have become invaded by annual grasses (Harrison et al. 2001; Harrison et al. 2003). The higher fertility levels are credited with promoting exotic dominance on these soils (Huenneke et al. 1990).

Elevated plant-available soil N has been linked to success of invasive annual grasses (Rickard et al. 1973; Bashkin et al. 2003; Brooks 2003; Lowe et al. 2003). Several greenhouse and field experiments with cheatgrass (*Bromus tectorum* L.) show greater growth of cheatgrass with additions of NH_4 and NO_3 (Dakheel et al. 1993; Hoopes and Hall 2002). Cheatgrass displays increased competitive ability with elevated N levels when compared to the native perennial grass, blue grama (*Bouteloua gracilis*) (Lowe et al. 2003) and the exotic perennial grass, desert wheatgrass (*Agropyron desertorum)* (Yoder and Caldwell 2002). Similar results have been observed in California with ripgut brome (*Bromus diandrus*) (Hoopes and Hall 2002). Initial increases in N generated a strong response in cheatgrass growth; further additions produced little additional response (Yoder and Caldwell 2002; Lowe et al. 2003). This result suggests that there are essential nutrients or resources other than N limiting further increases in the competitive ability of cheatgrass.

Fire can alter soil N by increasing the availability of NO_3 and NH_4 which sometimes promotes the spread of nonnative species. Studies in ponderosa pine (*Pinus ponderosa*) forests and pinyon-juniper (*Pinus edulis-Juniperus osteosperma*) woodlands have documented increases in several nonnative species after especially severe fires, including Dalmatian toadflax (*Linaria dalmatica*) (Korb et al. 2004; Dodge et al. 2008), common mullein (*Verbascum thapsus*) (Korb et al. 2004; Bataineh et al. 2006), and cheatgrass (Floyd et al. 2006; Keeley and McGinnis 2007; Laughlin and Fulé 2008; McGlone et al. 2009). Increased plant-available N has been reported in association with some post-fire nonnative invasions (Korb et al. 2004).

While these studies give a limited portrait of soil N levels that facilitate invasion, they suggest inferences about the role of N in exotic plant invasion. The N-amendment experiments, coupled with information on N paucity in serpentine soils, suggest that N-poor soils are less likely to support a nonnative community. Assuming other essential nutrients quickly limit growth after N-limitation has been released, greater overall soil fertility would have a positive influence on invasion success. This supports the theory that ruderal species, such as invasive grasses and forbs, have better establishment and growth in areas that have higher soil fertility (Grime 1977; Chapin 1980).

Phosphorus

While few studies have examined the role of plant-available P (HPO_4) in facilitating invasion, Bashkin et al. (2003) determined that cheatgrass occurred preferentially in sites with higher total P. Miller et al. (2006a) showed cheatgrass performance increased in the presence of elevated P, though the effect varied depending on the growth stage of the plants and moisture availability. Since P occurs in low concentrations in serpentine soils, it is reasonable to assume this nutrient is important in limiting invasion by annual grasses (Huenneke et al. 1990). Greenhouse studies have shown increases in cheatgrass biomass production with additions of P (Dakheel et al. 1993; Gundale et al. 2008). Results have been inconsistent, however, with some studies reporting little or no response to P amendments, depending on soils used in the experiment (Gundale et al. 2008; Miller and Seastedt 2009).

Changes in soil properties after invasion

Several studies have compared soil N and P dynamics in non-invaded areas with recent invasions and/or long-term invasions. These studies suggest that plant-available N

and P can be altered by invasion, but there are few data available for both pre- and post-invasion periods. Most information comes from adjacent non-invaded communities that are assumed to have similar soil properties as the invaded areas prior to invasion. This assumption may or may not be accurate and is often unverifiable.

Nitrogen

Changes in the N cycle after invasion are reliant on several, often interdependent, factors including changes in the spatial distribution of plant biomass, soil moisture, soil biota, and alterations to the local disturbance regime (e.g., accelerated fire cycle). It is difficult to make broad generalizations, however, due to differing soil – plant interactions across soil types and invasive species. Research results have reflected this variability, with different studies reporting the full range of possible outcomes from increased N cycling, to no change, to decreased N cycling after invasion.

Several studies have shown a positive correlation between total soil N and nonnative species richness or cover (Bolton et al. 1993; Stohlgren et al. 1999; Bashkin et al. 2003; Booth et al. 2003b; Korb et al. 2004; Belnap et al. 2005). In some instances, this has been attributed to pre-invasion conditions (Belnap et al. 2005) or relocation of N in the soil profile through increased litter production, increases in soil biota near the surface, and the lack of N storage in annual nonnative species when compared to native perennials (Bolton et al. 1993; Booth et al. 2003b). In the Mohave Desert, Schlesinger et al. (1996) detected pre-invasion spatial distribution patterns in soil N in a cheatgrass monoculture, 14 years after invasion. Furthermore, Svejcar and Sheley (2001) reported no differences in total soil N after 40 years of cheatgrass dominance when compared to adjacent non-invaded sites. In Montana, soil N was slightly lower under spotted knapweed (*Centaurea*

stoebe ssp. *micranthos*) plants, when compared to native perennial grasses, but the trends were inconsistent (Hook et al. 2004). In a thinned forest in Colorado, N additions to the soil increased Canada thistle (*Cirsium arvense*) populations (Miller and Seastedt 2009).

Some nonnative annual grass species can indirectly influence soil N by accelerating or perpetuating the fire cycle, such as cheatgrass, red brome (*Bromus rubens*), or Arabian schimsus (*Schismus arabicus*) (Brooks et al. 2004). These species may have the greatest impact on total N in the soil. While fire often generates an immediate pulse of plant-available N, the ecosystem experiences a loss of total N due to volatilization and biomass removal (D'Antonio and Vitousek 1992). Fire does not, however, always lead to a strong increase in nonnative species (Moore et al. 2006; Fowler et al. 2008; Kuenzi et al. 2008; Fornwalt et al. 2010). In Washington, Dodson and Peterson (2009) detected few nonnative invasive plants in forests three years after burning in a wildfire even when N fertilizer was applied.

Nonnative invasion can alter the N cycle, though the response is varied (Fig. 1.1). Most of the available information on invasion-induced changes in the N cycle comes from research on cheatgrass in the Great Basin. Several studies have shown increased N mineralization in cheatgrass-dominated areas, when compared to neighboring native communities (Bolton et al. 1993; Booth et al. 2003b). This result was not consistent, however, with lower rates of N mineralization detected in arid Utah in cheatgrass-dominated areas due to higher C:N and lignin:N ratios than the native species (Evans et al. 2001). Other studies detected increased levels of NO_3 in cheatgrass-dominated areas (Norton et al. 2004; Sperry et al. 2006; Chambers et al. 2007). Increased N mineralization and soil NO_3 have been attributed to accelerated nutrient cycling through rapid

decomposition of cheatgrass litter (Norton et al. 2004; Sperry et al. 2006) and changes in the distribution and diversity of soil flora (Bolton et al. 1993; Belnap and Phillips 2001; Belnap et al. 2005). Additionally, temporal interannual variation in soil N cycling, consistent with the life cycle of cheatgrass, has been detected. That is, soil N is depleted at germination, turnover rates are rapid during growth, and NO_3 accumulates in the soil after cheatgrass senesces, prior to germination (Booth et al. 2003b).

Nonnative plant interactions with the N cycle are less studied in species other than cheatgrass and the results are varied. In California, areas invaded by two nonnative annual grasses, slender oat (*Avena barbata*) and soft brome (*Bromus hordeaceus*), had double the gross nitrification rate and an increased abundance of NH_4–oxidizing bacteria in the soil when compared to native grassland soils (Hawkes et al. 2005). Areas dominated by the annual forb, burningbush (*Bassia scoparia)*, had increased soil N mineralization rates (Vinton and Burke 1995), while medusahead *(Taeniatherum caput-medusae)* dominated areas can have reduced N mineralization (Trent et al. 1994).

Phosphorus

Less is known about the influence of nonnative plant invasions on soil – P interactions (Fig. 1.2). Amelioration of P limitation commonly occurs by liberating calcium (Ca)-bound P from the soil through wetting or rhizosphere acidification (Marschner 1995, Hinsinger 1998). Nonnative plant – soil moisture relations are complex, with some studies showing a general decrease in soil moisture in invaded areas, other studies showing high levels of spatial and temporal variability (Melgoza et al. 1990; Booth et al. 2003b; Gerlach 2004; Kulmatiski et al. 2006). The role of invasion-induced alterations in water availability and plant-available P is not well-established. Plants

generally alter soil P availability through biofeedback mechanisms such as acidic root exudates or leachates from plant litter (Cannon et al. 1995, Watt and Evans 1999, Callaway and Aschehoag 2000, Duda et al. 2003, Miller et al. 2006a,b).

Several nonnative plant species generate root exudates that can free Ca-bound P. For example, diffuse knapweed (*Centaurea diffusa*) releases an allelopathic compound (8-hydroquinoline) from its roots which increases uptake of P in diffuse knapweed, but can significantly reduce P uptake and biomass production of native perennial grasses (Callaway and Aschehoag 2000). The related species, spotted knapweed, exudes (±)-catechin, an allelopathic chemical that can also free Ca-bound P (Watt and Evans 1999). While the elevated plant-available P is generally available for root uptake by all local plants, spotted knapweed is highly efficient at absorbing and assimilating P (Thorpe et al. 2006). There is evidence that root exudates are involved in cheatgrass – native perennial grass P dynamics, but the relationship is not clear. Some research suggests that cheatgrass liberates Ca-bound P through root exudates (Miller et al. 2006a,b). Other research suggests there may be a multi-organism interaction where root exudates from a native perennial grass, James' galleta (*Pleuraphis jamesii*) promote soil biotic activity that liberates calcium-bound P. Thus, James' galleta can indirectly facilitate P-uptake by cheatgrass (Belnap and Sherrod 2009).

Leaf tissue leachates, such as oxalates, can also increase soil plant-available P. Two annual nonnative forbs, halogeton (*Halogeton glomeratus*) and Russian thistle (*Salsola tragus*), produce oxalates in leaf tissue which leaches into the soil via rain and snow. Soils under both these species have higher plant-available P than soils under neighboring species (Cannon et al. 1995, Duda et al. 2003). While plant-available P may

increase in areas invaded by Russian thistle, total P may decline due to removal of litter through wind and rain (Allen 1993).

Plant competition plays an important role in depleting the pool of labile P and some nonnative invaders can acquire P at higher rates than their native competitors. For example, the perennial nonnative grass, smooth brome *(Bromus inermis)* and a related annual grass, red brome, can reduce plant-available P at faster rates than neighboring species, although the competitive advantage is not manifested against all native species (Yoder and Nowak 2000, Wang et al. 2004). The depletion of soil P by nonnatives is not ubiquitous, however. LeJuene et al. (2006) detected no change in plant–available P after removal of diffuse knapweed, suggesting that diffuse knapweed was not having an adverse impact on the availability of P in the soil.

Altering soil nutrients to manage invasions

Nitrogen

The dependence of some nonnative plant species on highly fertile soils is viewed as a potential "Achilles' heel" that can be exploited by land managers to mitigate invasions. One proposed mechanism for altering soil fertility, and thereby reducing nonnative plant dominance, is to reduce N levels through carbon amendments. The addition of C to the soil promotes bacterial growth which should, at least temporarily, bind up much of the available N in the soil (Fig. 1.1). The addition of sucrose as a C source can be effective at reducing nonnative plant biomass and density. In Utah, cheatgrass density and biomass were reduced by nearly half during the growing season following C addition (Beckstead and Augspurger 2004). A similar study in Colorado detected an approximately 20% reduction in cheatgrass cover in response to sucrose soil

amendments (Rowe et al. 2009). Another study in Colorado reported reduced relative growth rates in diffuse knapweed with sucrose amendments, but survival rates were higher (Suding et al. 2004). Canada thistle cover was also reduced by sucrose amendments in thinned Colorado forests (Miller and Seastedt 2009). Sucrose, however, is expensive and impractical for use over large landscapes. Furthermore, little is known about how long this treatment will be effective or how often it must be reapplied before the nonnative species will be reduced to subordinates in the system. Sawdust has been proposed as an alternative, less expensive, form of C-amendment. This, however, has not been effective. In California, there was no change in community composition to sawdust additions in a diverse nonnative forb and grass community (Corbin and D'Antonio 2004). Similar results were seen with cheatgrass in the Sierra Nevada (Keeley and McGinnis 2007) and a mixed community of nonnative forbs and grasses in eastern Oregon (Huddleston and Young 2005). These results are likely due to slow decomposition of woody material. Conversely, woodchip amendments from pinyon-juniper woodland mastication treatments increased cheatgrass cover after 2.5 years (Owen et al. 2009). The authors suggest this was due to increased soil moisture under the woodchips. Results have been improved by the combination of sawdust and sucrose. In Colorado, diffuse knapweed biomass was reduced by almost 40% with sucrose and sawdust amendments (Reever Morghan and Seastedt 1999). Soil NO_3 and NH_4 were significantly reduced in the first month after treatment, but the differences faded thereafter. Furthermore, the biomass of western wheatgrass (*Pascopyrum smithii*), the target native grass for the study, did not increase 3 years after treatment.

Phosphorus

It has been proposed that nonnative populations can be reduced through induced P limitation. The tendency for plant available P to bond with calcium to form recalcitrant compounds can be used to limit P availability in the soil (Fig. 1.2). Most of this research has been conducted on cheatgrass, though some work has been done on other nonnatives. In a laboratory germination and emergence experiment, reduction of P through the application of $CaCl_2$ reduced cheatgrass emergence by approximately 20 – 50% depending on concentration and soil type (Belnap et al. 2003). Furthermore, additions of CaO or Fe_2O_3 significantly reduced cheatgrass emergence in soils from under native perennial grasses, but not in soils from invaded areas. None of the soil amendments caused significant reductions in germination rates of James' galleta grass seeds. In Colorado ponderosa pine forests, P reduction treatments with gypsum reduced the relative growth rate of diffuse knapweed, but also increased the survival rate of individuals (Suding et al. 2004). In the same region, P reduction treatments had no significant influence on Canada thistle cover (Miller and Seastedt 2009). Field experiments in Utah with applications of CaO to reduce P availability had no significant effect on cheatgrass establishment, growth or biomass (Miller et al. 2006a), nor did it significantly reduce phosphate levels in the soil (Miller et al. 2006b). This is consistent with research in the Sierra Nevada, where P limitation through $CaCO_3$ additions did not reduce cheatgrass cover (Keeley and McGinnis 2007).

Conclusions

The availability of soil N and P can play an important role in invasion dynamics, particularly in environments with low nutrient availability such as arid and semi-arid

ecosystems of the western US. Many invaders are ruderal species that require the immediate availability of essential nutrients. They must also be able to out-compete neighboring species for these nutrients. The competitive ability of nonnative species can vary depending upon the identity and life stage of the native competitor. Once a species successfully invades an area, the invader can have a strong influence on soil N and P dynamics. These influences have the potential to perpetuate the persistence of the invasion. Researchers and land managers have attempted to use the strong interrelationship between invaders and available N and P to mitigate invasions. This has met with some experimental success, but practical applicability has been limited.

There are many unanswered questions regarding nutrient dynamics and invasion ecology. Our understanding of nonnative plant – soil N and P interactions is based primarily on research with annual grasses. While this is understandable due to the ubiquity of these species and the severity of their invasions, there are also perennial grasses and perennial and annual forbs that pose important threats of invasion as well. These functional groups tend to be less studied. A broader understanding of the role of soil N and P in facilitating the establishment and spread of nonnative species will enhance our ability to predict and, hopefully, mitigate new invasions. Furthermore, while our understanding of post-invasion changes in soil N and P cycling has increased in recent years, there are still many unexplained inconsistencies in experimental results. For example, why do some invasions increase N and P availability while others have a negative or neutral influence? Is this a species- or site-specific response? How do post-invasion changes in soil nutrient cycles influence persistence of invasion and native species recovery? Lastly, can we successfully manipulate soil N and P in order to reduce

invasions? While some studies have shown promise, particularly with N reduction techniques, the results have been inconsistent and are often impractical for widespread application.

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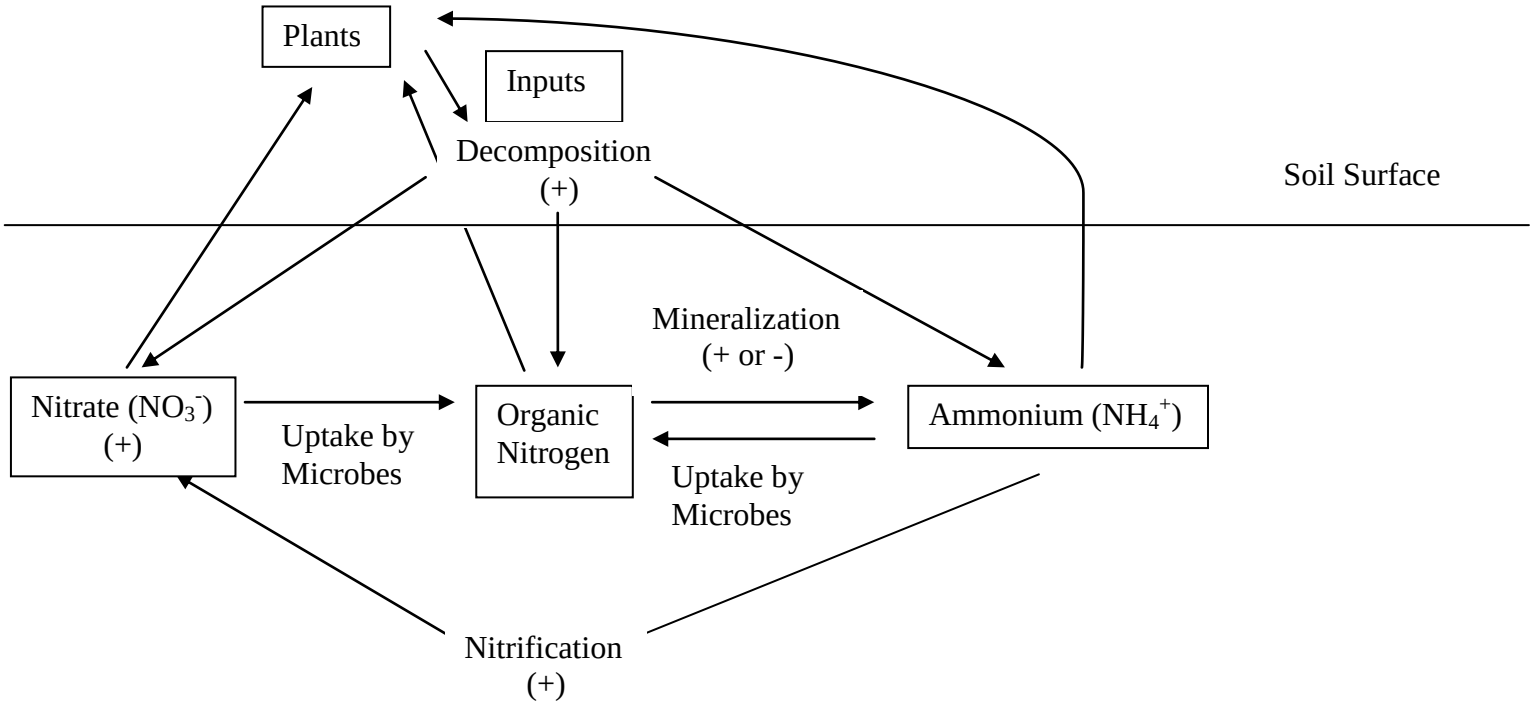

Figure 1.1 – Diagram of subsurface N dynamics that are influenced by nonnative plant invasions. Studies have typically reported increased N mineralization (Bolton et al. 1993; Vinton and Burke 1995; Booth et al. 2003b; Norton et al. 2004; Sperry et al. 2006), although reduced N mineralization has also been reported (Trent et al. 1994; Evans et al. 2001). Nitrification rates can also increase (Booth et al. 2003b; Hawkes et al. 2005). Litter decomposition can also increase (Norton et al. 2004; Sperry et al. 2006). Nitrate pools in invaded areas (Norton et al. 2004; Sperry et al. 2006; Chambers et al. 2007), though that can vary temporally based on the phenology of the invasive species (Booth et al. 2003b). Also, soil biota can be altered by invasion (Bolton et al. 1993; Belnap and Phillips 2001; Belnap et al. 2005; Hawkes et al. 2005).

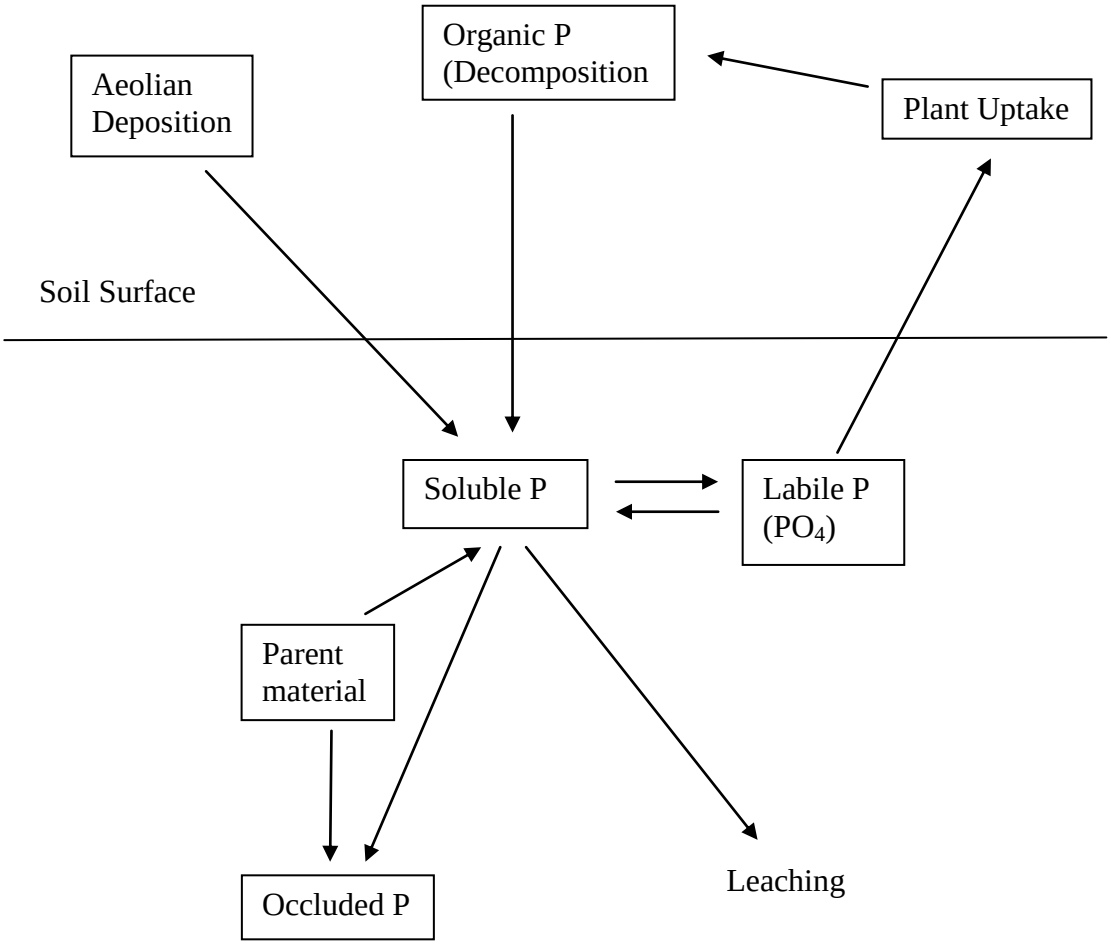

Figure 1.2 – Schematic diagram of the soil P cycle, showing pools (boxes) and fluxes (arrows). Nonnative plant species commonly alter this cycle by increasing the plant-available (labile) P by releasing Ca-bound P from the soluble P pool with acidic root exudates (Watt and Evans 1999; Callaway and Aschehoag 2000; Miller et al. 2006 a,b; Thorpe et al. 2006) or leachates from aboveground material (Cannon et al. 1995; Duda et al. 2003). Additionally, the pool of plant available P can be reduced if the nonnative is a better competitor for the resource (Yoder and Nowak 2000; Wang et al. 2004; LeJeune et al. 2006).

Chapter 2
Invasion resistance and persistence: established plants win, even with disturbance and high propagule pressure

Abstract Disturbances and propagule pressure are key mechanisms in plant community resistance to invasion, as well as persistence of invasions. Few studies, however, have experimentally tested the interaction of these two mechanisms. We initiated a study in a southwestern ponderosa pine (*Pinus ponderosa* Laws.)/bunch grass system to determine the susceptibility of remnant native plant communities to cheatgrass (*Bromus tectorum* L.) invasion, and persistence of cheatgrass in invaded areas. We used a 2 x 2 factorial design consisting of two levels of aboveground biomass removal and two levels of reciprocal seeding. We seeded cheatgrass seeds in native plots and a native seed mixture in cheatgrass plots. Two biomass removal disturbances and sowing seeds over three years did not reverse cheatgrass dominance in invaded plots or native grass dominance in non-invaded native plots. Our results suggest that two factors dictated the persistence of the resident communities. First, differences in pretreatment levels of plant-available soil nitrogen and phosphorus favored the dominant species in each community. Second, bottlebrush squirreltail (*Elymus elymoides* (Raf.) Swezey) was the dominant native herbaceous species on the study site. This species is typically a poor competitor with cheatgrass as a seedling, but is a strong competitor when mature. Our study shows that soil properties and established plants can buffer the influences of disturbance and elevated propagule pressure on cheatgrass invasion.

Keywords: Arizona, *Bromus tectorum*, Disturbance, *Elymus elymoides*, Nitrogen, Phosphorus, Propagule Pressure

Introduction

Plant invasions can be triggered by the interaction of different mechanisms including disturbance, increased propagule pressure, climate, resource availability, and plant functional traits (Elton 1958; Hobbs and Huenneke 1992; Lonsdale 1999; Mack et al. 2000). While disturbances and/or propagule pressure are often considered principal drivers of invasion (Von Holle and Simberloff 2005; Lambrinos 2006; Eschtruth and Battles 2009), some native plant communities remain resistant to nonnative plant encroachment. Ecologists have proposed that invasions are driven by fluctuations in resource availability that cause temporal and/or spatial variations in niche availability regardless of the resource-liberating mechanism (Stohlgren et al. 1999; Davis et al. 2000). Thus, successful invasions require synchrony of resource availability and presence of a nonnative species capable of exploiting the resource (Tilman 2004). Furthermore, propagules of the nonnative species must be present in sufficient quantity to capture resources to the detriment of the native community.

Empirical experimental studies of community invasibility in natural ecosystems are rare and results are often inconsistent. Beckstead and Augspurger (2004) demonstrated that competition with native perennial grasses and a lack of soil disturbance were important for resistance to cheatgrass (*Bromus tectorum* L.) invasion in a Great Basin ecosystem, while high nitrogen availability was the main factor in sustaining cheatgrass dominance. Thomsen et al. (2006), however, found that reduced competition with established species had little influence on perennial grass invasion in a California coastal prairie. Instead, timing of precipitation and propagule pressure were most important in overcoming invasion resistance. Chambers et al. (2007) determined that the most

influential factors driving invasion in Great Basin sagebrush communities varied depending on elevation, but sites with the highest cover of perennial grasses had the greatest resistance to invasion, regardless of elevation.

Cheatgrass is an annual grass from the Mediterranean Region that has invaded large expanses of the western United States and is considered a strong transformer species (*sensu* Richardson et al. 2000). Cheatgrass typically invades semi-arid grass- and shrublands where it often becomes the dominant species (Mack 1981; Knapp 1996). Cheatgrass out-competes many native perennial grass seedlings, but performs worse when competing with mature native plants (Booth et al. 2003a; Lowe et al. 2003; Humphrey and Schupp 2004). Furthermore, cheatgrass success is promoted by high soil nutrient levels, particularly nitrate, which often increases in the soil immediately after fire (Link et al. 1995; Lowe et al. 2003; Beckstead and Augspurger 2004; Gundale et al. 2008).

Cheatgrass is considered to be poorly adapted to coniferous forests. Its growth and fecundity are limited by shade, low air and soil temperatures causing reduced cheatgrass emergence and survivorship, and disturbance to the extant understory is often necessary for cheatgrass establishment (Pierson and Mack 1990a,b; Pierson et al. 1990). Recently, however, cheatgrass has become increasingly prevalent in ponderosa pine (*Pinus ponderosa* Laws.) forests of the American West (Crawford et al. 2001; Laughlin and Fulé 2008; Keeley and McGinnis 2007; McGlone et al. 2009b). This prevalence is associated with recent increases in fire and anthropogenic disturbance in ponderosa pine forests (Gildar et al. 2004; Keeley 2006; Fowler et al. 2008). In 2002-03, a ponderosa pine forest ecological restoration project in the Uinkaret Mountains of northern Arizona became

heavily invaded by cheatgrass immediately following a severe drought and wet autumn and winter (McGlone et al. 2009a). Cheatgrass populations expanded from being a minor component of the vegetation to becoming the dominant understory species over much of the landscape. The invasion was, however, heterogeneously distributed with many remnant areas of intact native vegetation containing little or no cheatgrass.

In 2004 we initiated an experiment in the Uinkaret Mountains to determine the susceptibility of native-dominated communities to nonnative plant invasion, the persistence of recently established dominant nonnative populations, and the role of disturbance and elevated propagule pressure in shifting community dominance. We promoted a cheatgrass invasion by disturbing the native vegetation through aboveground biomass removal, increasing cheatgrass seed availability, and a combination of these treatments. Aboveground biomass removal has promoted cheatgrass spread in the Great Basin (Beckstead and Augspurger 2004; Chambers et al. 2007), although cheatgrass invasion can occur even without disturbance when sufficient seeds are available and climatic conditions are conducive to cheatgrass growth (Belnap and Phillips 2001; Evans et al. 2001). Additionally, we attempted to reduce cheatgrass dominance through similar manipulations of cheatgrass-dominated areas: aboveground biomass removal of cheatgrass and increased availability of native species seeds. Lastly, we compared edaphic properties between adjacent native- and cheatgrass-dominated areas to evaluate whether soil nutrient content and structure varied between community types. We hypothesized that 1) disturbance to the native-dominated community would reduce the community's resistance to invasion, particularly in presence of enhanced cheatgrass propagule pressure, and 2) disturbance to the cheatgrass-dominated community would

reduce the community's resistance to encroachment by native species, with enhanced native propagule pressure increasing native species and cover.

Methods

Study Site

Mt. Trumbull is in the Uinkaret Mountains in northwestern Arizona (36° 22' N, 113° 8' W). The elevation ranges from 2,000 to 2,250 m. Soils are predominantly Inceptisols derived from basalt and occasionally volcanic cinders (Jorgensen 2004). Annual precipitation averages 412 mm, but varied from 276 to 831 mm during the four study years (Fig. 1). Frontal storms generate snow and rain in winter, accounting for approximately 50% of annual average precipitation, and monsoonal thunderstorms from July through August account for 21%. Winter precipitation for 2004-07 was below average, while monsoonal rain was average or above average during the study.

The study site is part of a landscape-scale ecological restoration research project. The overstory was thinned to emulate pre-1870 forest structure. Trees extant before 1870 were retained including replacement trees for remnant evidence of trees (i.e. - stumps) that died in the interim. Merchantable timber was removed from site, remaining slash was lopped and scattered, and treated areas were broadcast burned. Thinning was conducted from 1996 to 1999 and the slash and understory were burned from 1996 to 2001 (Figure 2). After treatment, tree density averaged 399 trees ha^{-1} and mean basal area averaged 18.9 m^2 ha^{-1} (see Roccaforte et al. 2009 for further details).

Overstory vegetation was dominated by ponderosa pine and Gambel oak (*Quercus gambelii* Nutt.). Additional tree species include New Mexico locust (*Robinia neomexicana* Gray), pinyon pine (*Pinus edulis* Engelm.), Utah juniper (*Juniperus*

osteosperma (Torr.) Little), and quaking aspen (*Populus tremuloides* Michx.). Dominant shrubs include big sagebrush (*Artemisia tridentata* Nutt.), wax currant (*Ribes cereum* Dougl.), and Utah serviceberry (*Amelanchier utahensis* Koehne). Principal perennial grasses are muttongrass (*Poa fendleriana* (Steud.) Vasey), bottlebrush squirreltail (*Elymus elymoides* (Raf.) Swezey), and western wheatgrass (*Pascopyrum smithii* (Rydb.) A. Löve). There is a diverse community of annual and perennial forbs. There were no annual grasses detected except for nonnative annual bromes, predominantly cheatgrass.

Experimental Design

We established 10 blocks of 8 plots; each block contained one replicate of each treatment in each community type. Treatments were randomly assigned to plots. Each replicate treatment plot was 2 x 2 m with a 1-m buffer. Within each plot, ten randomly located, 20- x 50-cm subplots were sampled for a total sampled area of 1 m^2 per plot. Plots were excluded from cattle grazing by a 4- x 4-m exclosure of three-strand barbed wire.

The blocks were established across a 2.5-km wide cheatgrass-invaded area. Within each block the elevation, aspect, slope, soil type, and time since restoration treatment (thinning and prescribed burning) were the same. Time-since-treatment ranged from 4 – 8 years. The eight plots were located within a 100-m radius of the center of each block. The criteria for native plot selection were: location within 20 m of a cheatgrass-dominated area, and having a native perennial grass cover of >35% and cheatgrass cover of $\leq$1% of the total plant cover within the plot. Cheatgrass plots were within 20 m of a native plot and had to have more cheatgrass cover than the cover of all native species combined. Additionally, plots in both native- and cheatgrass-dominated areas had to show evidence

of having been prescribed burned (i.e. - charred wood). We randomly assigned treatments within each block of each community type.

We used a 2 x 2 factorial experimental design with two levels of aboveground biomass removal and two levels of seeding. The biomass removal (clipped) treatment removed all aboveground live biomass from the plots at the onset of the experiment. The seeding treatment consisted of adding bottlebrush squirreltail, western wheatgrass, and silver lupine (*Lupinus argenteus* Pursh) seeds to cheatgrass-dominated plots and cheatgrass seed to native-dominated plots. The 2 x 2 factorial design generated four treatment combinations in each community type: 1) untreated control, 2) clipped, 3) seeded, and 4) clipped and seeded.

Experimental Treatments

We removed all aboveground vegetation from clipped plots twice: in late summer 2004 after August vegetation measurements and in late spring 2005, before May vegetation measurements. Clippings were timed to coincide with maximum aboveground biomass of native perennials (late summer 2004) and cheatgrass (May 2005). Additionally, most cheatgrass plants were flowering during the May 2005 clipping treatment. In the second clipping, no species that we experimentally seeded were removed from clipped and seeded plots in either community, regardless of whether the plants were seedlings or resprouted from root stock. All vegetation was clipped at ground level and removed from the site.

We seeded three times: fall 2004, spring 2005 and fall 2006. For native plots, we seeded 5g of cheatgrass seed per plot each time, a rate consistent with BLM seeding practices of native species for the Mt Trumbull Ecological Restoration project (Moore et

al. 2003). This equates to approximately 200 seeds m^{-2} per seeding for a total of approximately 600 seeds m^{-2} for the entire study. We collected seeds for the 2004 and 2005 seedings at Mt. Trumbull in July 2004. Seeds for the 2006 seeding were collected at Mt. Trumbull in July 2006. Cheatgrass seed germination averaged 92% in lab germination trials at 25°C. For cheatgrass plots we seeded 5g of native seed with equal amounts by weight of bottlebrush squirreltail, western wheatgrass, and silver lupine. This equated to an average of 65 bottlebrush squirreltail, 40 western wheatgrass, and 40 silver lupine seeds m^{-2} per seeding, for a total of ~435 seeds m^{-2} for the entire study. Germination for bottlebrush squirreltail, western wheatgrass, and silver lupine was 60%, 38%, and 24%, respectively, in laboratory tests. Silver lupine seeds were scarified prior to seeding by abrading the seed coat for five seconds with sandpaper (Baskin and Baskin 2001).

Vegetation Measurements

Each sampling period we measured plant canopy cover by species, cheatgrass density, species richness, and cheatgrass frequency. We visually estimated cover of all shrubs and herbaceous plants in each 20- x 50-cm subplot. Percent cover was measured using a 10- x 10-cm template to estimate 1% of a square meter, and was summed across the 10 subplots. Total plant cover was calculated by summing total cover over all species. Additionally, we counted the number of individual cheatgrass plants in each subplot and summed across the 10 subplots for a plot-level total. Species richness was based on plot-level presence/absence. Cheatgrass frequency was calculated on a scale of 0-10, equal to the number of subplots per plot containing at least one cheatgrass plant. Plant species were identified to species unless reliable field identification was not possible; in such

cases, plants were identified to genus. Plant nomenclature and nativity follows USDA-NRCS (2009).

We measured vegetation twice each year: in late May when cheatgrass was at maximum aboveground biomass and flowering, and in late August when many native plants were at maximum aboveground biomass. Pretreatment measurements were made in 2004. Post-treatment measurements were made in 2005, 2006 and 2007. Individual cheatgrass plants were counted in all subplots in all years except 2006.

In spring and summer 2007 we measured cover and then harvested all above-ground biomass from the subplots. We clipped biomass from half of the subplots in May 2007 and the other half in August 2007. The subplots clipped in May were excluded from the August 2007 measurements. Biomass was sorted by species, oven-dried at 70°C for 2 days, and weighed.

Soil Samples

We collected soil samples in late August 2004 at the onset of the study and coincident with maximum aboveground biomass of native perennials and initiation of cheatgrass germination. We collected two soil samples from each plot. One sample was tested for pH immediately after collection using a Denver Instrument UB-5 pH meter. The second sample was returned to the laboratory for other analyses. For each sample, soils were collected at four fixed locations within the 1-m buffer zone between the plots and exclosure fences to a depth of 10 cm using a 4-cm diameter soil corer. The four core samples were composited for analysis, sieved through a 2-mm sieve, and all coarse organic material was removed. From each sample of the second soil collection, a 10-g subsample was placed in 100 ml of KCl solution and stored on ice for analysis of nutrient

concentration. Samples were analyzed for nutrient concentration at the Colorado Plateau Analytical Laboratory at NAU following Sparks (1996).

Statistical Analyses

Changes in plant community variables were tested using repeated measures MANOVA. We visually assessed multivariate normality (Q-Q plots of the residuals) and tested for univariate normality (Shapiro-Wilk test) and homogeneous variances (Levene's test). Total richness data and all cover data except cheatgrass cover consistently met the assumptions. For analyses with significant year x treatment interactions, we tested for year and treatment differences using Tukey's HSD test. Cheatgrass cover, frequency, and density data were non-normal and transformations did not address non-normality. For these variables we used Kruskal-Wallis signed ranks tests. For analyses with significant year x treatment interactions, we tested for year and treatment differences using a two-sample Wilcoxon signed ranks test with a Bonferroni correction. The August sampling period occurred during the cheatgrass germination period and thus incompletely measured cheatgrass presence and cover. Therefore, we only analyzed cheatgrass data from May. Because the 2005 data collection immediately followed the clipping treatment, we excluded those data from all analyses, although we present them graphically for descriptive purposes.

For August 2007, only the five subplots not clipped in May 2007 were measured. Richness data for this sampling period was therefore on a 0.5 m^2 scale. To determine the amount this underestimated richness calculated at the 1 m^2 scale used in all other measurements, we used August 2004-2006 data to generate species accumulation curves

using EstimateS software (Colwell 2006); this revealed that 75-86% of all species were captured by five subplots.

We compared soil nutrient concentrations between community types using ANOVA. Most soil data required either log or cube-root transformation to meet ANOVA assumptions. Due to the number of soil analyses conducted, we used a Bonferroni correction to control for possible Type I errors. All analyses except for the species accumulation curves were conducted using JMP 8.0 software (SAS Institute 2008).

Results

The influence of disturbance and cheatgrass propagule pressure in native-dominated community resistance to invasion

The native-dominated community was highly resistant to invasion regardless of treatment. Cheatgrass cover responded positively to the seeding and clipping treatment, although cheatgrass cover remained low (< 4%) throughout the experiment (Fig. 3A). Cheatgrass cover increased significantly from pretreatment levels in 2004 only in the clipped and seeded plots in 2006. The application of additional seed significantly increased the frequency of cheatgrass in 2006, but this increase was no longer detectable by 2007 (Figure 3B). Cheatgrass frequency significantly decreased after 2004 in the clipped treatment and was present on only three of the 10 plots by 2007. Cheatgrass density did not change significantly throughout the study (data not shown). In general, nonnative species were uncommon in the native-dominated community. Besides cheatgrass, the only other nonnative species were prickly lettuce (*Lactuca serriola* L.), Kentucky bluegrass (*Poa pratensis* L.), tumblemustard (*Sisymbrium altissimum* L.), and

yellow salsify (*Tragopogon dubius* Scop.). Of nonnative species other than cheatgrass, Kentucky bluegrass had the highest cover (1.1%) on any one plot.

We detected no treatment effect for total cover in either the May or August measurements for the native-dominated community (Fig. 4A & B). In both sampling periods, there was a significant year effect, with total cover increasing from 2004 to 2006. In May, cover returned to pretreatment levels by 2007, while in August cover continued to increase. Total cover consisted of almost entirely native species with bottlebrush squirreltail accounting for 40-100% of total cover in both May and August (Fig. 4C & D). In both May and August there was a significant treatment effect for bottlebrush squirreltail cover, with the clipped and seeded treatment resulting in reduced cover. There was also a significant year effect for bottlebrush squirreltail cover in both May and August, with greater cover after treatment than pretreatment. There was no detectable treatment effect on final biomass in either sampling period in 2007.

Over the course of the study we detected 68 species in the native-dominated community, with 53 of them observed in May and 51 observed in August. May species richness decreased by nearly half over the course of the study, regardless of treatment (Fig. 4E). By May 2007, plots averaged only 4 species m^{-2}. Nonnative species, typically cheatgrass, accounted for an average of <1 species m^{-2}. There was a significant time x treatment interaction for August species richness (Fig. 4F). The clipped plots had a significant reduction in species richness between 2004 and 2007, while the seeded plots had a significant increase between the same years. The consistent annual reduction in species richness observed in May did not occur in August. As in May, an average of <1 nonnative species m^{-2} occurred; cheatgrass was most common; others were purslane

(*Portulaca oleracea* L.), yellow salsify, and common mullein (*Verbascum thapsis* L.) The greatest cover of nonnative species excluding cheatgrass on any one plot was 1.8% for common mullein.

The influence of disturbance and native propagule pressure on the persistence of cheatgrass

By the end of our study, cheatgrass continued to dominate the invaded community regardless of treatment for measurements in May. We detected a significant year by treatment interaction for cheatgrass cover in May. The interaction was the result of the clipped treatments and clipped and seeded treatments in 2006 having significantly lower cover than the control and seeded treatments (Fig. 5A). By 2007, cheatgrass cover remained lower in the two treatments that included clipping, but variability was high and differences were not significant. Cheatgrass density was not significantly affected by treatments, but more than doubled from 2004 to 2007 (Fig. 5B). Since cheatgrass cover was roughly the same in 2004 and 2007, the cheatgrass population in 2007 consisted of more numerous, but smaller plants.

In May, the treatment by year interaction was significant for total cover (Fig. 6A). The control and seeded treatments showed a significant increase from 2004 to 2006, with no significant difference between 2004 and 2007. There was no significant treatment response in May of any year in the clipped or clipped and seeded treatments. The trends in total cover were similar to cheatgrass cover, since cheatgrass accounted for approximately 75% of all cover throughout the study (Figs. 5A & 6A). There was no significant treatment effect for total cover in August, but there was a significant year effect, with total cover increasing throughout the study (Fig. 6B). Seeded species cover

did not differ by treatment in May and remained below 8% for all treatments and years (Fig. 6C). In May of both 2004 and 2007, seeded species cover accounted for approximately 7% of total species cover. In August, however, there was a significant annual increase in seeded species cover regardless of treatment, suggesting that the increased cover was driven by natural recruitment, not our experimental seeding (Fig. 6D). There was no detectable treatment effect for either May or August biomass in 2007 (data not shown).

We observed a total of 75 species on the cheatgrass plots over the course of the study, seven more than on the native plots. In May, we observed 60 species on the cheatgrass plots including 10 nonnative species and in August we observed a total of 62 species, again with 10 nonnative species. Cheatgrass was the dominant nonnative species on all cheatgrass-invaded plots, regardless of sampling season. In May, maximum cover for the other nonnative species ranged from 0.25% for black bindweed (*Polygonum convolvulus*) to 8% for tumblemustard. In August, nonnative species were typically rare with low cover on the cheatgrass-dominated plots, although common mullein cover on one plot was 15.75%. Treatment and year significantly affected total richness in May, with richness in clipped, and clipped and seeded plots having nearly double the number of species as in the seeded and control in 2006 and 2007 (Fig. 6E). In August, species richness was not significantly affected by treatment, but varied significantly over time with all treatments increasing by 1 – 2 species m^{-2} from 2004 to 2007 (Fig. 6F).

Soil properties

We detected three significant differences in concentrations of soil nutrients between native- and cheatgrass-dominated communities at the onset of the study in 2004 (Table

1). Concentrations differed for phosphate (PO_4), total nitrogen (N) and nitrate (NO_3). Of these nutrients, NO_3 differed the most, with concentrations in cheatgrass-dominated soils two times higher than in native-dominated soils. Soil texture was similar in the two communities and averaged approximately 66%, 11%, and 23% for sand, silt, and clay, respectively.

Discussion

Both native- and cheatgrass-dominated communities on Mt. Trumbull were resistant to shifts in species dominance despite two aboveground biomass removal disturbances and elevated seed availability over the first three years of the study. Native-dominated communities were not only resistant to cheatgrass encroachment; cheatgrass was nearly extirpated from the plots by 2007 regardless of treatment. In May 2007, cheatgrass-dominated areas returned to pretreatment levels for most parameters of community composition. Thus, clipping had only short-term effects on cheatgrass-dominated communities in May when cheatgrass was at maximum aboveground biomass. The only change in community dominance we detected was in the cheatgrass-dominated community in August when cheatgrass was germinating and contributed little plant cover. By August 2007, bottlebrush squirreltail cover was approximately equal to cheatgrass cover. The resistance of the two communities to sustained changes in composition may be due, in part, to community differences in soil nutrient concentrations. Total N, NO_3, and PO_4 were higher in the cheatgrass-dominated areas than in native-dominated areas. Our study cannot, however, quantify the contribution of soil nutrients versus resident native species in limiting cheatgrass invasion.

Invasion resistance in the native-dominated community

The clipping and seeding treatments in this study were unsuccessful in inducing cheatgrass establishment in the native-dominated community. Cheatgrass seeding treatments resulted in an initial increase in cheatgrass cover and frequency, but following this initial pulse cheatgrass was actually less prevalent in 2007 than before treatment in 2004. The initial increase in cheatgrass lends some support for hypothesis #1 - disturbance to the native-dominated community would reduce community resistance to invasion, particularly in presence of elevated cheatgrass propagule pressure. The predicted increase in cheatgrass was, however, only transient.

While we did not expect our treatments to create a complete shift in dominance from native species to cheatgrass, the failure of increased disturbance and propagule pressure to increase cheatgrass establishment was unexpected. Disturbance and propagule pressure are considered main drivers of invasion (Elton 1958; Hobbs and Huenneke 1992; Williamson 1996). Recent field research has supported this theory, with propagule pressure often being more important than disturbance in promoting invasion (Von Holle and Simberloff 2005; Lambrinos 2006; Eschtruth and Battles 2009). Furthermore, since native plots were in close proximity to cheatgrass-dominated plots (20 m), and differences in disturbance history, weather influences, soils, and geography were minimal, it is unlikely that our results were confounded by extraneous differences between communities.

Several factors may explain our inability to experimentally induce cheatgrass establishment in the native-dominated community. One factor that may have regulated cheatgrass success during the study is precipitation. Cheatgrass seedlings are highly

susceptible to mortality through desiccation (Pierson and Mack 1990a). The last two winters of our study had below-average precipitation that may have limited cheatgrass performance. Furthermore, the native community on Mt. Trumbull was dominated by bottlebrush squirreltail, a species that is considered a strong competitor with cheatgrass. Bottlebrush squirreltail and its congeneric relative, big squirreltail (*Elymus multisetus* M.E. Jones), can limit cheatgrass establishment and spread (Booth et al. 2003a; Humphrey and Schupp 2004; Leger 2008). In a Great Basin shrub-steppe study, areas with >15% bottlebrush squirreltail cover almost completely excluded cheatgrass (Booth et al. 2003a). Like cheatgrass, bottlebrush squirreltail is physiologically active very early in the growing season, which may explain its ability to compete with cheatgrass (Jones 1998). The effectiveness of bottlebrush squirreltail as a competitor, however, seems to be dependent on plant life stage, with mature plants being strong competitors but seedlings unable to compete with cheatgrass (Humphrey and Schupp 2004).

Lastly, lower levels of plant-available N and P in soils of the native community may have favored native perennials over cheatgrass. As an annual species, cheatgrass generally has greater dependence on plant-available soil nutrients for successful establishment and persistence than perennial species (Marschner 1995). Past research has shown both soil nutrient concentration and native species competition to be important in regulating invasions (Link et al. 1995; Booth et al. 2003a; Chambers et al. 2007); possibly their combined influences provided both community resiliency and resistance to cheatgrass invasion in our study.

Persistence of cheatgrass in the invaded community

Cheatgrass cover in May was reduced by clipping in 2006, but the effect was transient and diminished in 2007. Furthermore, seeding with native species had no significant effect on any community characteristic of the cheatgrass-dominated community. This result gives limited support to hypothesis #2 - disturbance to the cheatgrass-dominated community would reduce the community's resistance to encroachment by native species, with enhanced native propagule pressure increasing native species cover. Specifically, our results partially support the hypothesis that the cheatgrass population would be reduced by disturbance, though only in the first two growing seasons after treatment. The results do not, however, support the hypothesis that seeding treatments would promote native species cover.

Cheatgrass has been highly persistent in many ecosystems after invasion (Mack 1981; Brandt and Rickard 1994; Knapp 1996). Numerous studies have examined the possibility of reducing dominance of cheatgrass, and other nonnative annual brome grasses, by mowing, seeding, soil nutrient reduction through carbon and other chemical amendments, and herbicide application (Hull Jr. and Stewart 1948; Belnap et al. 2003; Scoles et al. 2003; Davison and Smith 2007; Belnap and Sherrod 2009). While many techniques have temporarily reduced cheatgrass populations, most research suggests that long-term suppression of cheatgrass requires actively reducing cheatgrass and promoting perennial grasses, usually through seeding (Hull Jr. and Stewart 1948; Cox and Anderson 2004; Davison and Smith 2007). This approach was ineffective during three years of seeding and four years of measurements in our study. The failure of the seeded species, bottlebrush squirreltail, silver lupine, and western wheatgrass, to establish may be due to

inability as seedlings to compete with cheatgrass (Hull Jr. 1963; Lowe et al. 2003; Humphrey and Schupp 2004). The continued increase in seeded species cover in August measurements, however, suggests that the community dynamics may not be resolved. Interestingly, the increase in seeded species cover in August was independent of treatment, suggesting that natural re-establishment of the species contributed to their increased cover. While increases in seeded species cover were not detected in May by the end of the study, it is possible that continued increases in late-season native cover may reach a level that inhibits success of future cheatgrass generations.

One factor that may have contributed to the persistence of cheatgrass was the higher plant-available soil N and P concentrations in the cheatgrass plots compared to native plots prior to treatment. These nutrients are important in regulating cheatgrass competitive ability with native species (Dakheel et al. 1993; Booth et al. 2003b; Miller et al. 2006a; Belnap and Sherrod 2009). Elevated soil N is often associated with cheatgrass-dominated communities when compared to native communities (Bolton Jr. et al. 1993; Booth et al. 2003b; Belnap et al. 2005; Sperry et al. 2006). Most studies examining cheatgrass – soil N relationships have been conducted in the Great Basin Desert; little is known about these relationships in mountain forests. In addition to N, plant-available P often limits plant productivity (Elser et al 2007). Field research has shown a positive relationship between plant-available P and cheatgrass performance (Bashkin et al. 2003; Belnap et al. 2003; Miller et al. 2006a,b). Miller et al. (2006a) suggested that plant-available P was the primary limitation to cheatgrass performance in a southern Utah study. Additionally, cheatgrass may increase labile P in invaded soils through rhizosphere

acidification (Miller et al. 2006a,b). As with N, however, little is known about the role of P in regulating cheatgrass invasion in mountain forests.

This study cannot confirm a causal relationship between soil nutrients and species distribution and further research is necessary to determine whether the differences we observed in soil N and P regulated the heterogeneous distribution of cheatgrass on Mt. Trumbull. Nonetheless, our finding of an association between cheatgrass and high levels of plant-available soil N and P is consistent with other studies and supports the theory that cheatgrass success is greatest in patches with high plant-available soil N and P.

Conclusions

None of our hypotheses was fully supported by our data. First, we proposed that disturbance via complete clipping of aboveground biomass would increase cheatgrass cover and abundance on native-dominated plots, particularly in plots with an enhanced cheatgrass seed bank. Instead, we found the native community on Mt. Trumbull was resistant to further invasion regardless of treatment. This result suggests that factors governing invasion of native communities are complex and elevated disturbance and seed availability may not always result in invasion. Second, we proposed that disturbance to cheatgrass-dominated plots would reduce cheatgrass populations, with native seed amendments promoting native species cover. Cheatgrass populations were only slightly reduced by disturbance and native species failed to establish, even after nearly 500 seeds m^{-2} were sown over three years. The herbaceous understory at the study site was dominated by two grass species at the end of the study: bottlebrush squirreltail on native plots and cheatgrass on cheatgrass plots. This pattern may be the result of species-specific responses to spatial variation in plant-available soil N and P at the study site. We

conclude that shifts in dominant herbaceous communities at Mt. Trumbull could not be induced by disturbance and elevated seed availability. Instead, communities that were dominated by a single, highly competitive species, regardless of the nativity of that species, were resistant to changes in community dominance.

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Table 2.1 Soil nutrient content and pH in native and cheatgrass communities. Means are reported with one standard error of the mean in parentheses (n=40). F and P values are from one-way ANOVA. Boldface means within rows are significantly different with a Bonferroni adjusted α=0.004

Nutrient	Native	Cheatgrass	F	P
Total N (mg g^{-1})	**1.90 (0.10)**	**2.30 (0.10)**	**11.30**	**0.001**
NO_3 (mg g^{-1})	**0.0026 (0.0005)**	**0.0049 (0.0005)**	**17.51**	**<0.001**
NH_4 (mg g^{-1})	0.0036 (0.0003)	0.0042 (0.0003)	0.41	0.105
Total P (mg g^{-1})	1.57 (0.03)	1.67 (0.03)	4.92	0.03
PO_4 (mg g^{-1})	**0.062 (0.005)**	**0.092 (0.005)**	**22.51**	**<0.001**
K (mg g^{-1})	7.07 (0.15)	7.22 (0.15)	2.09	0.15
Ca (mg g^{-1})	8.16 (0.42)	8.96 (0.42)	2.93	0.09
Cu (mg g^{-1})	0.039 (0.0005)	0.038 (0.0005)	1.27	0.26
Fe (mg g^{-1})	5.57 (0.11)	5.31 (0.11)	4.48	0.04
Mg (mg g^{-1})	19.37 (1.27)	19.13 (1.27)	0.14	0.71
Mn (mg g^{-1})	0.96 (0.01)	0.94 (0.01)	1.59	0.21
Na (mg g^{-1})	6.84 (0.46)	5.31 (0.46)	4.63	0.04
Zn (mg g^{-1})	0.088 (0.002)	0.093 (0.002)	4.50	0.04
pH	6.54 (0.05)	6.63 (0.05)	2.41	0.13

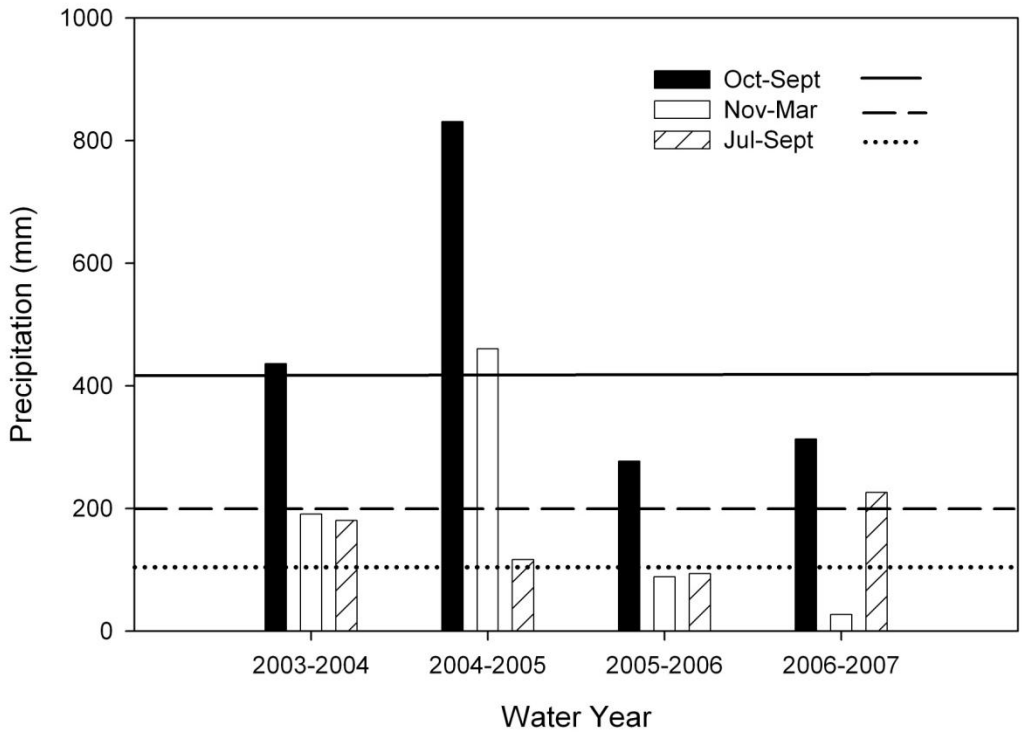

Fig. 2.1 Annual water year precipitation near the study site (Nixon Flats Remote Access Weather Station). Bars represent total water year (October to September), winter (November to March), and monsoonal (July to September) precipitation. The lines represent the 1992-2007 average precipitation. The solid line is the annual average, the dashed line is the winter average, and the dotted line is the monsoonal average

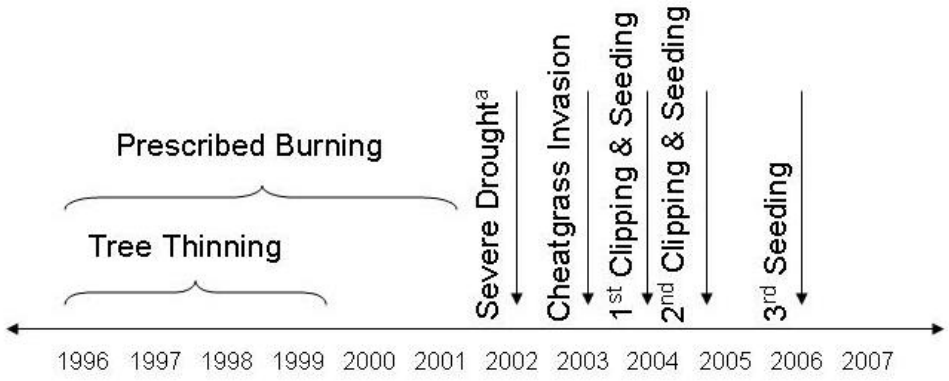

Fig. 2.2 History of restoration treatments, drought, cheatgrass invasion, and experimental clipping and seeding treatments at the Mt. Trumbull Ecological Restoration site since project inception in 1995. [a] From August 2001- August 2002, the site received 29% of average annual precipitation

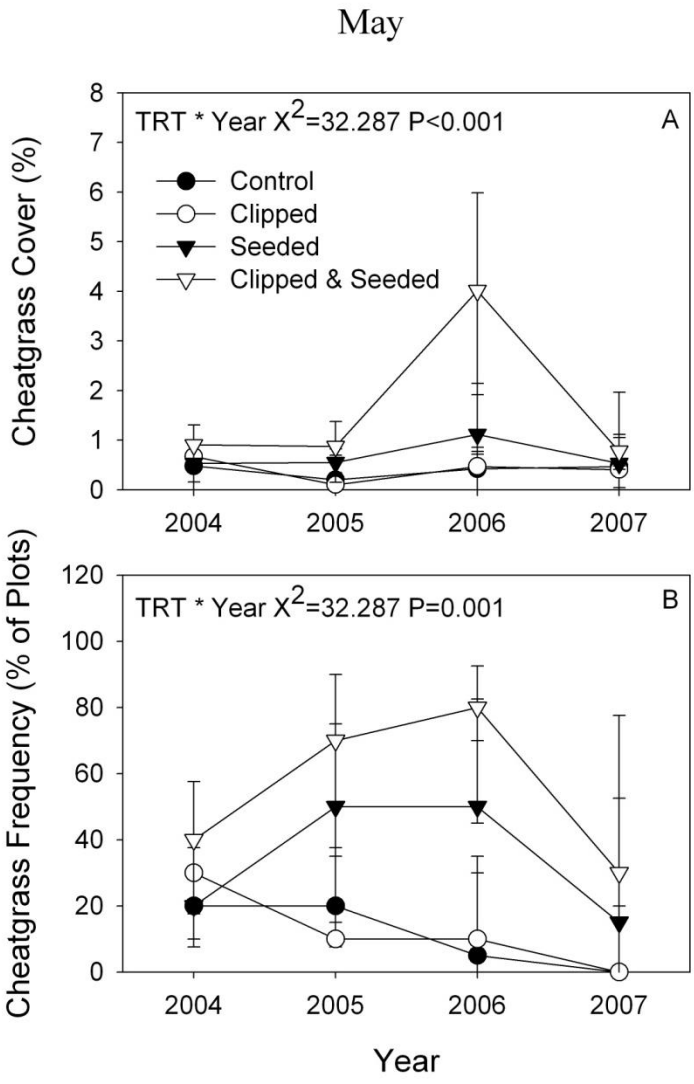

Fig. 2.3 Median cheatgrass cover (%) (A) and frequency (% of plots) (B) by treatment for the May measurements on native plots. Seeded treatments were sown with cheatgrass seed. Error bars represent 25th and 75th percentile. Significant Kruskal-Wallis signed ranks test results are listed in each panel (α=0.05). All 2005 data were excluded from statistical analysis because clipping occurred prior to measurements

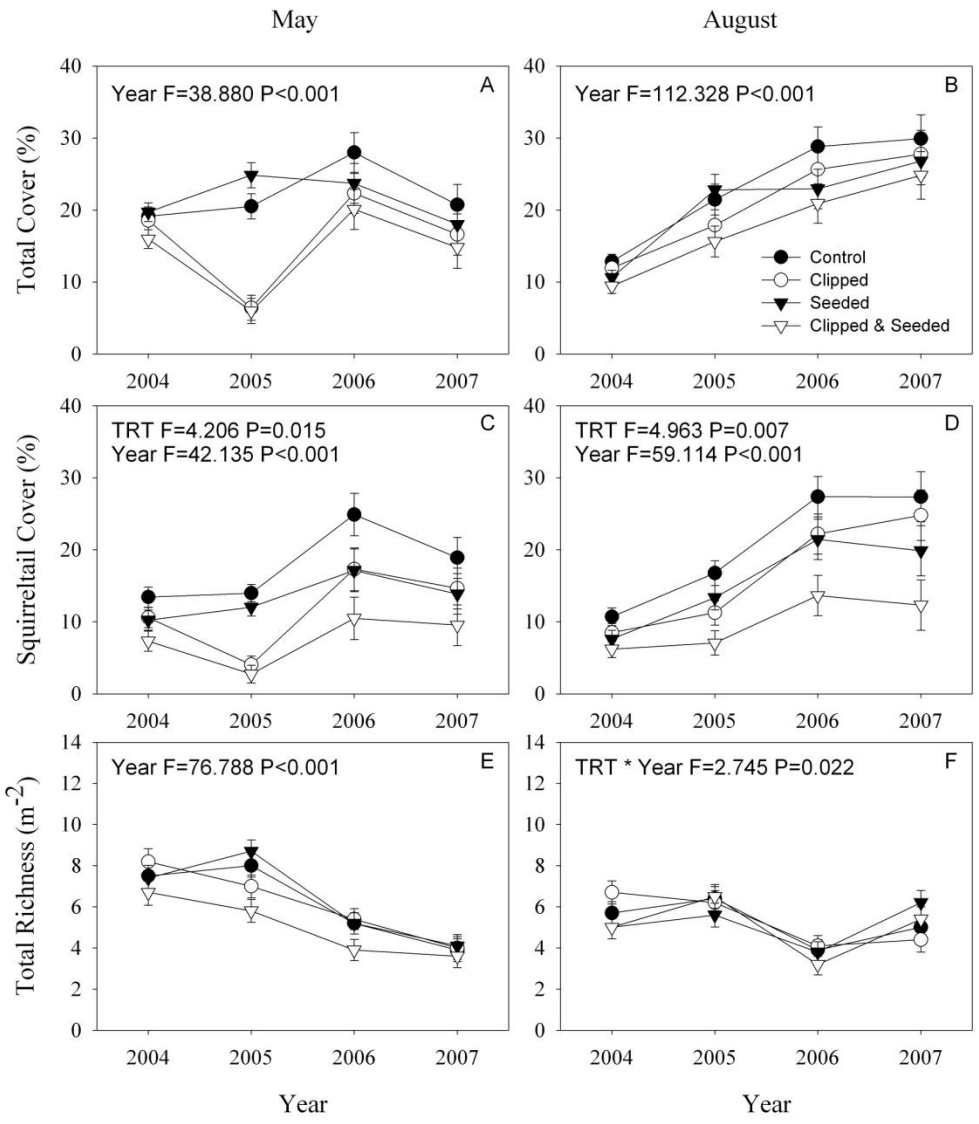

Fig. 2.4 Average total cover (%) (A, B), bottlebrush squirreltail cover (%) (C, D), and total richness m^{-2} (E, F) by treatment for May (A, C, E) and August (B, D, F) measurements on native plots. Seeded treatments were sown with cheatgrass seed. Error bars represent one standard error of the mean. Significant MANOVA results are listed in each panel (α=0.05). 2005 data were excluded from statistical analysis because clipping occurred prior to measurements

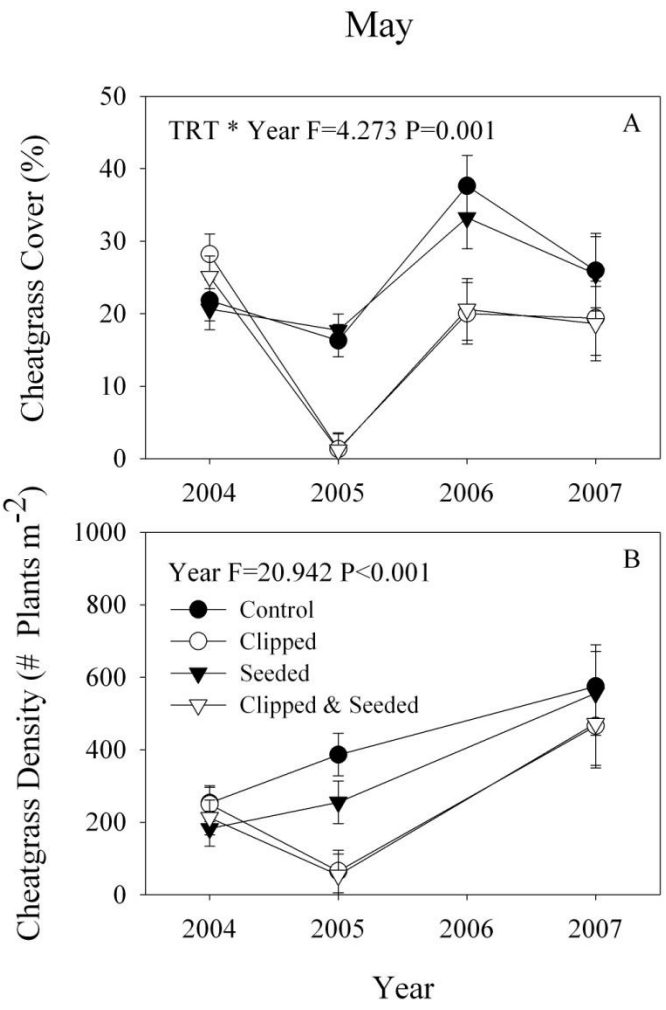

Fig. 2.5 Average cheatgrass cover (%) (A), and density (# plants m^{-2}) (B), by treatment for May measurements on cheatgrass plots. Seeded species include: bottlebrush squirreltail, western wheatgrass, and silver lupine. Error bars represent one standard error of the mean. Significant MANOVA results are listed in each panel (α=0.05). 2005 data were excluded from statistical analysis because clipping occurred prior to measurements

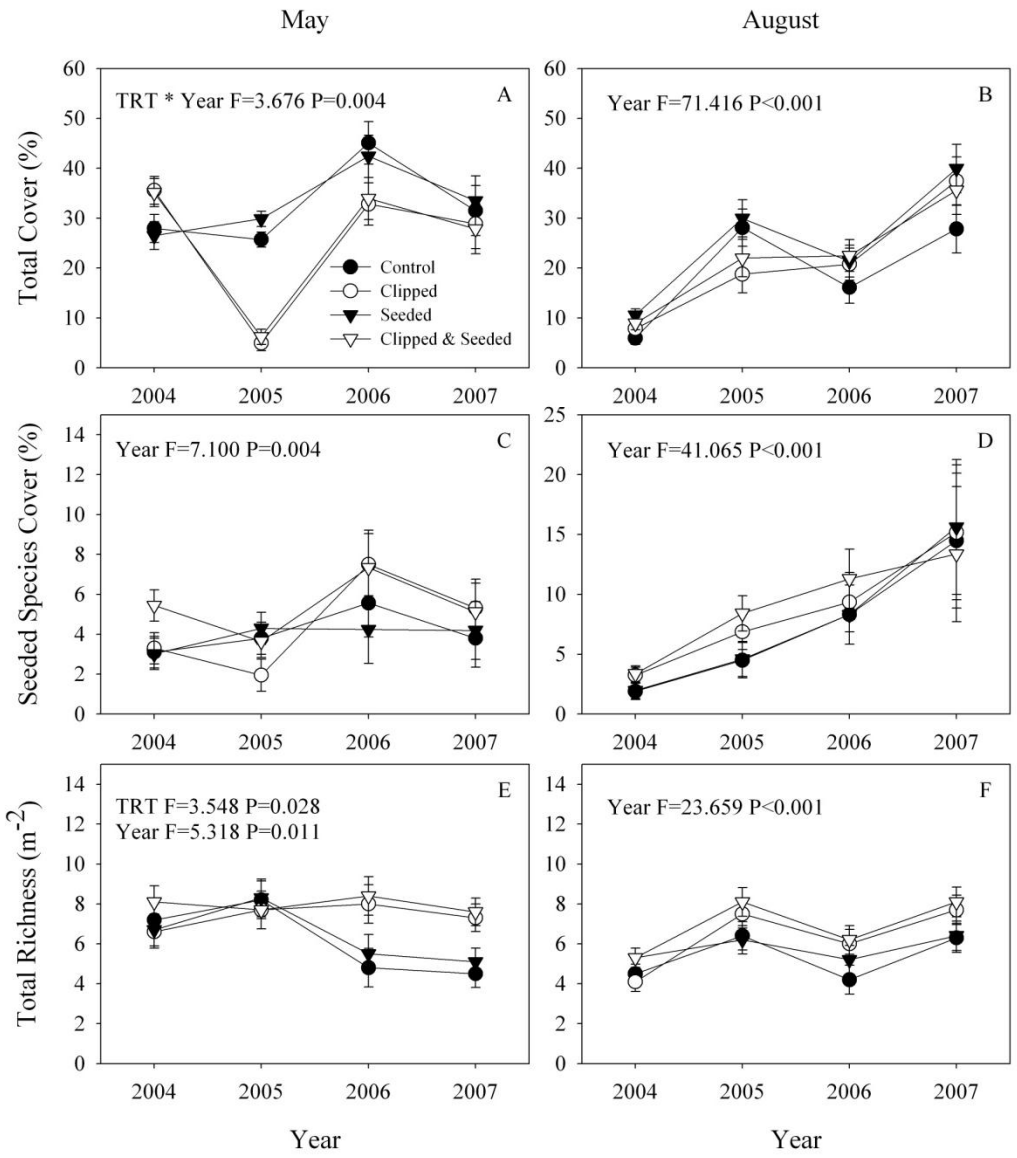

Fig. 2.6 Average total cover (%) (A, B), seeded species cover (%) (C, D), and total richness m^{-2} (E, F) by treatment for May (A, C, E) and August (B, D, F) measurements on cheatgrass plots. Seeded species include: bottlebrush squirreltail, western wheatgrass, and silver lupine. Error bars represent one standard error of the mean. Significant MANOVA results listed in each panel (α=0.05). 2005 data were excluded from statistical analysis because clipping occurred prior to measurements

Chapter 3
Changes in plant community composition in invaded and non-invaded plots at the onset of cheatgrass invasion

Abstract

Nonnative plant invasions have dramatically altered many ecosystems world-wide. Invasions can alter ecosystem structure, functions, and processes and these alterations can last for decades. While long-term invasions can result in a very different plant community than comparable non-invaded communities, little is known about changes in plant community composition shortly after invasion. In this study we examined changes in plant species composition in a ponderosa pine (*Pinus ponderosa*) forest in northern Arizona that was invaded by cheatgrass (*Bromus tectorum*) in 2003. We tested for temporal changes (2004-7) between paired invaded and non-invaded plots in species diversity, similarity, and richness. Furthermore, we used NMS ordinations to determine if adjoining invaded and non-invaded plots differed in plant species composition. The two plant community types differed in species composition at the onset of the study and continued to diverge in subsequent years. By 2007, the percentage of plant species occurring in both invaded and non-invaded plots declined by one-third compared to 2004. Species richness did not differ between community types in any year, but by the end of the study percent native species richness was lower in invaded plots in both spring and summer seasons. We conclude that cheatgrass invasion drove strong divergence in species composition five years after invasion.

Keywords: Arizona, Cheatgrass, Diversity, Invasion, Nonnative Species, Plant community, Species Composition

Introduction

Invasive, nonnative plant species can cause profound and potentially irreversible changes to ecosystems. Invasion can alter the natural environment at population, community, and ecosystem levels (Parker et al. 1999; Mack et al. 2000; Levine et al. 2003). Richardson et al. (2000) referred to these high-impact invasive species as "transformers" because they have lasting, multi-faceted impacts on the ecosystem. These ecosystem impacts can include changes in local biodiversity (Elton 1958; Williamson 1996), disturbance regimes such as the fire cycle (D'Antonio and Vitousek 1992; Brooks et al. 2004), and ecosystem processes (Crooks 2002; Hooper et al. 2005).

While invasion can reduce the abundance of native plant species, complete extirpation is less common, and native species often linger at low densities (Davis 2003; Gurevitch and Padilla 2004). This can lead to an actual increase in plant species richness following invasion at large spatial scales, with reductions in richness only occurring at localized scales (Parker et al. 1999). While transitions in dominant species in an invaded ecosystem are usually obvious and easy to measure, the loss or reduction in abundance of relatively rare species may have important consequences on an ecosystem if the species strongly influences ecosystem processes (Hooper et al. 2005).

Cheatgrass (*Bromus tectorum*) is an excellent example of a transformer species (Richardson et al. 2000). Cheatgrass is an annual grass from Eurasia that has invaded ~20 million ha of the Great Basin Desert in the western United States (Bradley and Mustard 2005) and occurs in all 48 contiguous United States (USDA, NRCS 2010). In areas where it has become the dominant species, cheatgrass has altered fire cycles (Whisenant 1990; Brooks et al. 2004), nutrient cycling (Evans et al. 2001; Belnap et al. 2005; Sperry et al.

2006), soil biota (Belnap and Phillips 2001), and the structure and composition of the vegetative community (Young and Evans 1978; Mack 1981; Knapp 1996). Cheatgrass is highly persistent after invasion, often dominating the plant community for decades (Mack 1981; Knapp 1996). Long-term cheatgrass dominance can substantially alter plant community composition (Knapp 1992; Brandt and Rickard 1994). While long-term consequences of invasion are important, plant community changes caused by invasive species at the onset of invasion initiate potential long-term changes (Grime 2001). Little is known about plant community compositional changes that occur at the onset of cheatgrass invasion.

We measured changes in plant species composition in paired invaded and non-invaded plots in a ponderosa pine (*Pinus ponderosa*) forest in the Uinkaret Mountains of northern Arizona that was recently invaded by cheatgrass. From 2002-2003, cheatgrass increased from a minor component of the understory vegetation to the dominant species in thinned and burned areas (see McGlone et al. 2009 for details). In 2004, we established a study to investigate changes in understory composition in native- and cheatgrass-dominated plots. We used a series of paired plots to examine differences in post-invasion plant species composition in neighboring invaded and non-invaded plots, and to quantify species changes over four consecutive years.

Methods

Our study site is in the Uinkaret Mountains in northwestern Arizona at elevations ranging from 2,000 to 2,250 m. Soils are predominantly Inceptisols derived from basalt parent material (Jorgensen 2004). Annual precipitation averages 412 mm, but varied from 276 to 831 mm during the four study years (Fig. 3.1). Frontal storms generate snow and

rain in winter, accounting for approximately 50% of annual average precipitation, and monsoonal thunderstorms from July through August account for 21%. Winter precipitation for 2005-2007 was below average, while monsoonal rain was average or above average for the duration of the study.

The study site is part of a landscape-scale ecological restoration research project. The overstory was thinned to approximate pre-1870 forest structure. All trees extant before 1870 were retained including replacement trees for all remnant evidence of trees (such as stumps) that died in the interim. Merchantable timber was removed from site, remaining slash was lopped and scattered, and treated areas were broadcast burned and seeded with a mix of native seeds. For further details on the restoration prescription, see Roccaforte et al. (2009). Thinning was conducted at the study site from 1996 to 1999 and the slash and understory was burned from 1996 to 2001. After burning, the treated areas were seeded at approximately 9 kg ha^{-1}. The seed mix varied annually. After treatment, tree density averaged 399 trees ha^{-1} and mean basal area averaged 18.9 m^2 ha^{-1} (Roccaforte et al. 2009).

The overstory vegetation in the area was dominated by ponderosa pine and Gambel oak (*Quercus gambelii*). Other tree species in the area included New Mexico locust (*Robinia neomexicana*), pinyon pine (*Pinus edulis*), Utah juniper (*Juniperus osteospermus*), and quaking aspen (*Populus tremuloides*). Dominant shrubs included big sagebrush (*Artemisia tridentata*), wax currant (*Ribes cereum*), and Utah serviceberry (*Amelanchier utahensis*). The dominant perennial grasses were muttongrass (*Poa fendleriana*), squirreltail (*Elymus elymoides*), and western wheatgrass (*Pascopyrum smithii*). Native annual grasses are limited to one rarely-occurring species: annual muhly

(*Muhlenbergia minutissima*). There is a diverse community of annual and perennial forbs.

We established 10 pairs of plots with each pair containing one plot in each community type (cheatgrass-dominated, hereafter "invaded", and native-dominated, "non-invaded"), with the non-invaded plots serving as controls. Each plot was 2 x 2 m with a 1-m buffer of similar habitat. Within each plot, ten 20- x 50-cm subplots were sampled for a total sampled area of 1 m^2 per plot. The location of the subplots was randomly selected. The plots were fenced with 3-strand barbed wire to exclude cattle grazing.

The plots were established across a 2.5-km band of the invaded landscape. Non-invaded plots were selected if they contained a substantial native perennial grass component (>35% of the vegetative cover) and had little or no cheatgrass within the plot area (no more than 1% of the vegetative cover). Invaded plots were established 20 m away from the paired non-invaded plots and had to have more cheatgrass cover than the cover of all native species combined in the plot. Additionally, each plot had to show evidence of having been prescribed burned, such as charred wood. Each pair had the same time since burning and post-burning seed mix composition, as well as similar slope, aspect, soil texture, and overstory canopy cover.

Vegetation Measurements

Each sampling period we measured aerial plant cover by species and recorded species richness. We visually estimated cover of shrubs and herbaceous plants in each 20- x 50-cm subplot, with a maximum of 10% cover per subplot, then summed across the 10 subplots. Cumulative total plant cover was calculated by summing the cover values of

individual species. Species richness was based on plot-level presence/absence. Plants were identified to species unless reliable field identification was not possible. In such cases, plants were identified to genus. Plant nomenclature and nativity were based on USDA, NRCS (2010).

We sampled vegetation twice a year: in late May when cheatgrass was at peak growth and in late August to capture peak native plant growth in response to late summer rain. The late August measurement period also coincided with cheatgrass germination. We sampled in each of four consecutive years from 2004 to 2007.

In 2007, we harvested aboveground biomass from the subplots. We clipped half the subplots in May 2007, immediately after measurement. The remaining subplots were harvested after the August 2007 measurements. The subplots harvested in May were not sampled in August. All biomass was oven-dried at 70°C for 48 hours and then weighed.

Statistical Analyses

We analyzed May and August data separately. Cover data were used for all analyses except richness. Because August 2007 data represented a partial data set, we excluded these data from species richness, diversity, and community composition analyses. In addition to total species richness, we calculated the percent native species richness per plot. We also calculated percent shared species (the Jaccard Similarity Coefficient (Cheetham and Hazel 1969) x 100) at the plot level (1 m^2) and across plots within invaded or non-invaded plots (10 m^2). Finally, we calculated the Shannon-Weiner index per plot. We used repeated measures MANOVA to analyze all plot-level variables, with year as the repeated factor. All significant year-by-invasion interactions were tested using a one-way ANOVA for within-year and between-invasion differences with a

Bonferroni adjustment based on number of years. Among-year differences were tested using Tukey's HSD post hoc analysis. MANOVA and ANOVA analyses were conducted using JMP software (version 8.0, SAS Institute 2008). We analyzed community-level differences using NMS. Ordinations were conducted using Sorenson distance measure with random starting configurations, 50 runs with real data, 200 iterations, and a 0.000010 stability criterion. The stress value of the final solution was compared to random solutions using a Monte Carlo test with 50 randomizations. All community analyses were conducted using PCOrd software (version 5.0, McCune and Mefford 2006).

Results

Cover in May differed significantly among years ($F = 11.84$; $P = 0.004$) and between communities ($F = 8.63$; $P = 0.02$), with consistently greater cover in invaded plots than in non-invaded plots. Average cover was highest in 2006, the year with the driest preceding winter (non-invaded plots = 28.0%; SE = 3.8 and invaded plots = 45.1%; SE =3.8). The 2007 May biomass data were highly variable, ranging from 7.2 to 45.2 g dry weight m^{-2} in non-invaded plots and 6.0 to 107.6 g dry weight m^{-2} in the invaded plots. Although not significant ($P = 0.184$), mean biomass was higher in invaded plots (43.46 g m^{-2}; SE = 6.5) than in non-invaded plots (25.4 g m^{-2}; SE = 6.5).

There was no significant difference in total species richness between invaded and non-invaded plots in May, though the average number of species declined significantly between 2004 and 2007 in both non-invaded and invaded plots ($F = 20.19$; $P = 0.001$). There was a significant community type-by-year interaction for percent native species richness ($F = 5.521$; $P = 0.03$), with native species accounting for significantly less of the

total richness in invaded plots in 2006 and 2007 (Fig. 3.2A). Percent shared species per plot (1 m^2) had a significant year effect ($F = 6.52$; $P = 0.001$), with significantly fewer shared species in the final two years of the study (Fig. 3.3A). At the 10 m^2 level, percent shared species declined from 59% in 2004 to 41% in 2007 (Fig. 3.3B). In May, non-invaded plots had six species that never occurred in invaded plots, while there were 11 species that were unique to invaded plots, including five nonnative species (Table 3.1). There was a significant year effect for the Shannon-Wiener index, with index values declining over time ($F = 25.69$; $P < 0.001$) (Fig. 3.4A). There was no significant community type effect for the Shannon-Wiener index. The NMS analysis of May data showed two distinct communities with community type accounting for 92% of the variability in the data (Fig. 3.5A).

Cover in August had a significant year-by-community type interaction ($F = 5.61$; $P = 0.03$), with significantly higher cover in non-invaded plots in 2004 and 2006 and no difference in 2005 or 2007. Mean cover values increased in time from 12.8% (SE = 1.0) in 2004 to 29.9% (SE = 5.0) in non-invaded plots and from 6.0% (SE = 1.0) in 2004 to 27.8% (SE = 5.0) in 2007 in invaded plots. Biomass in August ranged from 8.4 to 43.8 g dry weight m^{-2} (mean = 24.58 g dry weight m^{-2}; SE = 2.86) in non-invaded plots and 4.6 to 52.8 g dry weight m^{-2} (mean = 16.52 g dry weight m^{-2}; SE = 2.86) in invaded plots. As in May, there was no significant difference in biomass between invaded and non-invaded plots in August ($P = 0.176$).

There was also no significant difference in total species richness between invaded and non-invaded community types in August, but the year main effect was significant ($F = 73.42$; $P < 0.001$). Species richness increased from 2004 to 2005, but returned to near

2004 levels by 2006. There was a significant community type effect for percent native species richness ($F = 24.777$; $P = 0.001$), with native species accounting for significantly less of the total richness in invaded plots (Fig. 3.2B). Percent shared species per plot (1 m^2) had a significant year effect ($F = 5.06$; $P = 0.01$), with significantly fewer shared species in the final year of the study (Fig. 3.3A). At the 10 m^2 level, percent shared species declined from 52% in 2004 to 39% in 2006 (Fig. 3.3B). In August, non-invaded plots had seven species that never occurred in invaded plots, while there were nine species that were unique to invaded plots, including four nonnative species (Table 3.2). The Shannon-Wiener index was significantly higher ($F = 14.79$; $P = 0.001$) in invaded plots than in non-invaded plots (Fig. 3.4B). There was also a significant year effect for the Shannon-Weiner index ($F = 16.34$; $P < 0.001$) with the lowest value in both invaded and non-invaded plots occurring in 2006 (Fig. 3.4B). The NMS analysis of August data showed two distinct groups of communities with community type accounting for 62% of the variability in the data (Fig. 3.5B).

Discussion

Species richness was similar in invaded and non-invaded plots. Instead, cheatgrass invasion was associated with a shift in percent native species richness. In invaded plots, native species comprised a lower percent of the total richness than in non-invaded plots. In May, native species in invaded plots accounted for only 62% of the total richness in 2006 and 70% in 2007. In August, native species in invaded plots generally comprised < 75% of the total richness. A total of ten nonnative species occurred in invaded plots over the course of the study. Two of the nonnative species, smooth brome (*Bromus inermis*) and tall wheatgrass (*Thinopyrum ponticum*), were present on Mt.

Trumbull due to past range improvement seeding projects. The presence of the remaining eight species was likely due to accidental introductions such as seed mix contamination, the introduction of cattle from invaded winter grazing pastures, or seeds trapped in mud on vehicles. Of the nonnative species on Mt. Trumbull, two species, common mullein (*Verbascum thapsis*) and crossflower (*Chorispora tenella*), are currently listed as noxious in at least one U.S. state (UDSA, NRCS 2010). This contrasts with non-invaded plots where native species accounted for nearly 100% of the species richness. By the end of this study, cheatgrass was the only nonnative species to occur in the non-invaded plots and it was infrequent with low cover values.

There were also seasonal differences in total cover, diversity, shared species, and community composition between invaded and non-invaded community types. Average total cover measurements for spring and late summer were consistently between 20-30% in the non-invaded plots, across all years, with no consistent trend as to which season had the greatest cover values. In invaded plots, cover values were always greater in May than in August, with May measurements being as much as four-fold greater within the same year. The Shannon-Wiener diversity index for invaded and non-invaded plots was nearly identical across all years in May, but in August the plots diverged significantly. The two community types had fewer shared species in August for most years at both spatial scales. Furthermore, in the May community ordinations, invaded and non-invaded plots segregated into two clustered groups. In August, non-invaded plots remained clustered while invaded plots were more dispersed. We attributed the seasonal differences between the two community types to the winter annual growth habit of cheatgrass. In May, cheatgrass is at its growth maximum, accounting for approximately 75% of the total

cover in the invaded plots in any given year. The native perennial grass, bottlebrush squirreltail, dominated non-invaded plots in both May and August. In August, however, cheatgrass was just beginning to germinate and contributed low amounts to the total cover and aboveground biomass on any plot. The lack of cheatgrass dominance in August allowed subordinate species to have a stronger influence on the species composition.

Loss of biodiversity and local extirpation of species are a major concern in biological invasions (Elton 1958; Chapin et al. 2000; Mack et al. 2000; Levine et al. 2003; Gurevitch and Padilla 2004), particularly with strong transformer species such as cheatgrass (Richardson et al. 2000). Invaded plots on Mt. Trumbull supported a slightly different plant community at the onset of our study in May 2004, the second year after invasion. The differences in the two plant community types amplified over the four years of our measurements, with less than 50% of plant species occurring in both community types in either sampling season. The proximity of the invaded and non-invaded plots (20 m apart) and our efforts to standardize the plots for pre-invasion disturbance history, edaphic, climatic, and geographic factors, as well as minimizing post-invasion disturbances, minimize the likelihood that ecological factors extraneous to the cheatgrass invasion explain the differences in community composition. It is, therefore, reasonable to attribute the differences in species composition between community types to either the ecological conditions that facilitated or initiated the cheatgrass invasion, or as a response to cheatgrass dominance after the invasion.

Little is known about changes in community composition in response to recent invasions. This is an important aspect of invasion ecology since nonnative species dominance can suppress re-establishment of native species (Eliason and Allen 1997;

Humphrey and Schupp 2004). Chronosequence analysis of California disturbance sites dominated by annual nonnatives, including *Bromus* species, has shown that short-term community changes in response to disturbance can persist on a multidecadal scale (Stylinski and Allen 1999). Long-term monitoring of abandoned agricultural fields showed that early establishment by nonnative species prevented immigration by native species, thus altering the successional trajectory of the plant community (Yurkonis et al. 2005).

Our study demonstrates differences in plant species composition as a result of cheatgrass invasion after only five growing seasons. The vegetation changes we documented at Mt. Trumbull during the first five years of cheatgrass invasion could produce a trajectory of cascading effects that result in long-term ecosystem changes. Cheatgrass and other transformer species have significantly altered many of the ecosystems they have invaded (Vitousek and Walker 1989; Belnap and Phillips 2001; Evans et al. 2001; Crooks 2002; Belnap et al. 2005; Hooper et al. 2005; Sperry et al. 2006). By the end of our study, invaded plots had fewer nitrogen-fixing species, no longer contained some important nectar sources such as *Penstemon barbatus* and *Phlox longifolia*, and had a more depauperate native component compared with non-invaded plots.

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Table 3.1. Species occurring on the Mt. Trumbull research plots from May 2004-2007 exclusively in non-invaded or invaded plots within a given year. The X donates the year in which a species was detected in only one community type. If there is no X for a given year, then that species either was not detected or occurred in both community types that year. Boldface species were detected exclusively in one community type in all years it occurred in the study. All nomenclature is based on UDSA, NRCS (2010).

Community Type	Scientific Name	Common Name	Native?	2004	2005	2006	2007
Non-invaded							
	Allium bisceptrum	**Twincrest Onion**	**Y**		**X**		
	Arabis fendleri	Fendler's Rockcress	Y				X
	Calocortus nuttallii	**Sego Lily**	**Y**			**X**	
	Dracocephalum parviflorum	American Dragonhead	Y	X			
	Erigeron divergens	Spreading Fleabane	Y		X		
	***Lotus* species**[a]	**Trefoil**	**Y**		**X**		
	Packera multilobata	Lobeleaf Groundsel	Y			X	X
	Penstemon barbatus	Beardlip Penstemon	Y			X	X
	Phacelia heterophylla	Varileaf Phacelia	Y				X
	Poa fendleriana	Muttongrass	Y		X		X
	Quercus gambelii[b]	**Gambel Oak**	**Y**		**X**		
	Robinia neomexicana	**New Mexico Locust**	**Y**				**X**
	Senecio eremophilus	**Desert Ragwort**	**Y**			**X**	
Invaded							
	Artemisia carruthii	**Carruth's Sagewort**	**Y**	**X**			
	Artemisia tridentata	Big Sagebrush	Y	X			
	Bromus carinatus	**California Brome**	**Y**	**X**			
	Bromus inermis	**Smooth Brome**	**N**		**X**	**X**	
	Chorispora tenella	**Crossflower**	**N**	**X**			
	Conyza canadensis	**Canadian Horseweed**	**Y**	**X**			
	Dracocephalum parviflorum	American Dragonhead	Y			X	
	Galium aparine	**Stickywilly**	**Y**		**X**		
	Lactuca serriola	**Prickly Lettuce**	**N**	**X**	**X**	**X**	

Lappula occidentalis	Flatspine Stickseed	Y	X			X
Pascopyrum smithii	**Western Wheatgrass**	**Y**	**X**	**X**		**X**
Phacelia heterophylla	Varileaf Phacelia	Y		X		
Poa pratensis	**Kentucky Bluegrass**	**Y**				**X**
Polygonum douglasii	Douglas' Knotweed	Y				X
Thinopyrum ponticum	**Tall Wheatgrass**	**N**	**X**	**X**	**X**	**X**
Tragopogon dubius	Yellow Salsify	N				X
Verbascum thapsus	**Common Mullein**	**N**			**X**	**X**

[a] Genera that could not be identified at the species level were assumed to be native. It is possible that nonnative members of the genus could be present.

[b] Tree species were only included if they were < 137 cm in height

Table 3.2. Species occurring on the Mt. Trumbull research plots from August 2004-2007 exclusively in non-invaded or invaded plots within a given year. The X donates the year in which a species was detected in only one community type. If there is no X for a given year, then that species either was not detected or occurred in both community types that year. Boldface species were detected exclusively in one community type in all years it occurred in the study. All nomenclature is based on UDSA, NRCS (2010).

Community Type	Scientific Name	Common Name	Native?	2004	2005	2006
Non-invaded						
	Eriogonum pharnaceoides	Wirestem Buckwheat	Y	X		X
	Koeleria macrantha	**Prairie Junegrass**	**Y**	**X**		
	***Lotus* species**[a]	**Trefoil**	**Y**	**X**		
	Nama dichotomum	**Wishbone Fiddleleaf**	**Y**		**X**	**X**
	Packera multilobata	Lobeleaf Groundsel	Y			X
	Penstemon barbatus	Beardlip Penstemon	Y			X
	Phlox longifolia	Longleaf Phlox	Y			X
	Pinus ponderosa[b]	**Ponderosa Pine**	**Y**		**X**	
	Poa fendleriana	**Muttongrass**	**Y**		**X**	
	Robinia neomexicana	**New Mexico Locust**	**Y**	**X**		**X**
	Symphotricum falcatum	**White Prairie Aster**	**Y**	**X**		
Invaded						
	Bromus carinatus	**California Brome**	**Y**	**X**	**X**	**X**
	***Carex* species**[a]	**Sedge**	**Y**		**X**	
	Chenopodium species[a]	Goosefoot	Y	X		
	Conyza canadensis	**Canadian Horseweed**	**Y**	**X**		**X**
	Dracocephalum parviflorum	American Dragonhead	Y			X
	Erigeron divergens	Spreading Fleabane	Y			X
	Gayophytum diffusum	Spreading Groundsmoke	Y			X
	Lactuca serriola	**Prickly Lettuce**	**N**		**X**	**X**
	Lappula occidentalis	**Flatspine Stickseed**	**Y**		**X**	**X**
	Lepidium densiflorum	**Common Pepperweed**	**Y**		**X**	
	Mirabilis decepiens	Broadleaf Four O'clock	Y	X		X

Pascopyrum smithii	Western Wheatgrass	Y		X	X
Penstemon barbatus	Beardlip Penstemon	Y			
Phacelia heterophylla	Varileaf Phacelia	Y		X	
Sisymbrium altissimum	**Tall Tumblemustard**	**N**	**X**		
Thinopyrum ponticum	**Tall Wheatgrass**	**N**	**X**	**X**	**X**
Tragopogon dubius	**Yellow Salsify**	**N**			**X**
Verbascum thapsus	Common Mullein	N	X		X

[a] Genera that could not be identified at the species level were assumed to be native. It is possible that nonnative members of the genus could be present.

[b] Tree species were only included if they were < 137 cm in height

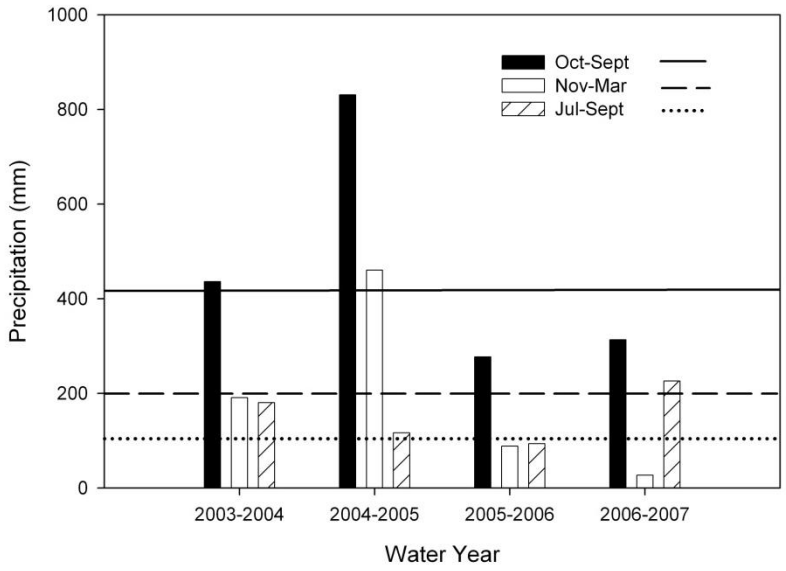

Fig. 3.1. Annual water year precipitation near the study site (Nixon Flats Remote Access Weather Station). Bars represent total water year (October to September), winter (November to March), and monsoonal (July to September) precipitation. The lines represent the 1992-2007 average precipitation. The solid line is the annual average, the dashed line is the winter average, and the dotted line is the monsoonal average.

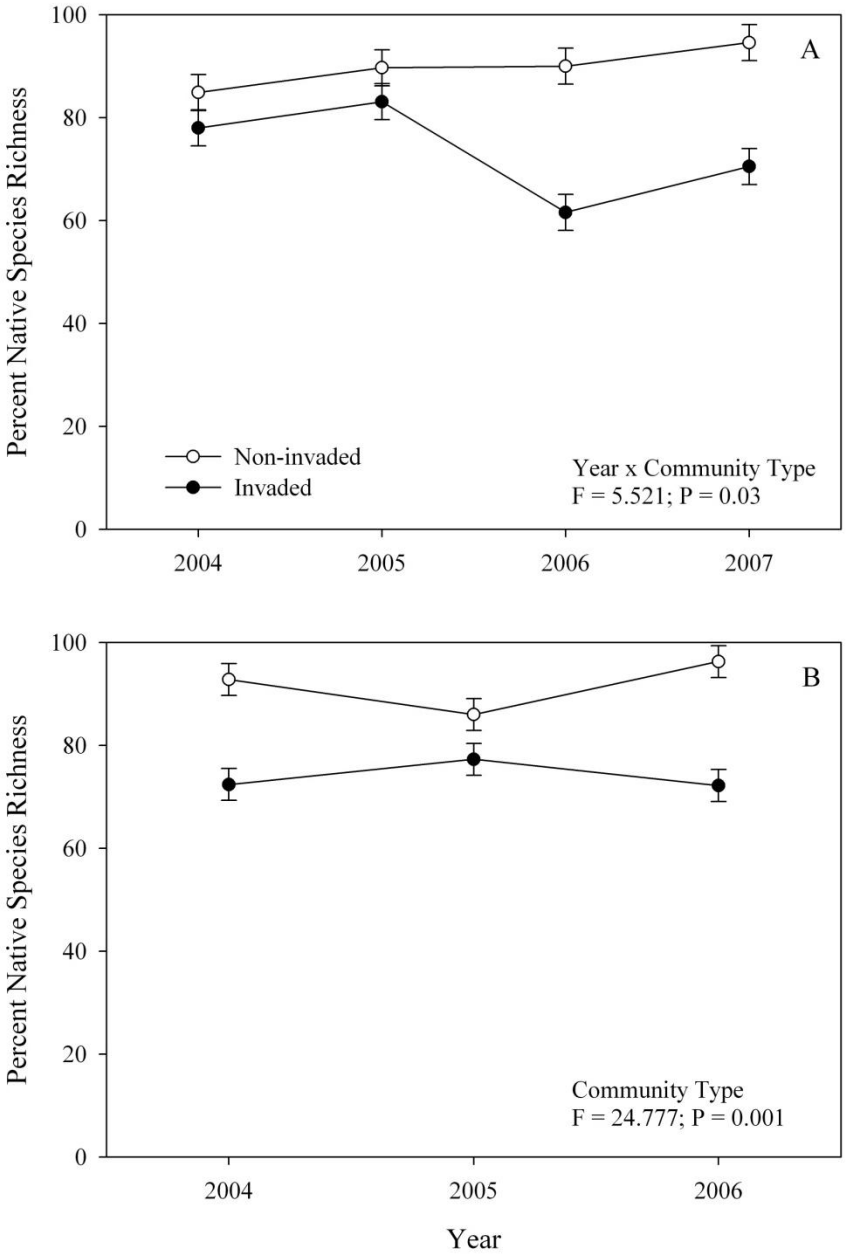

Fig. 3.2 – Average percent native species richness in May (A) and August (B) for invaded and non-invaded community types. Significant repeated measures MANOVA results are shown in lower right corner (α=0.05). Error bars represent one standard error.

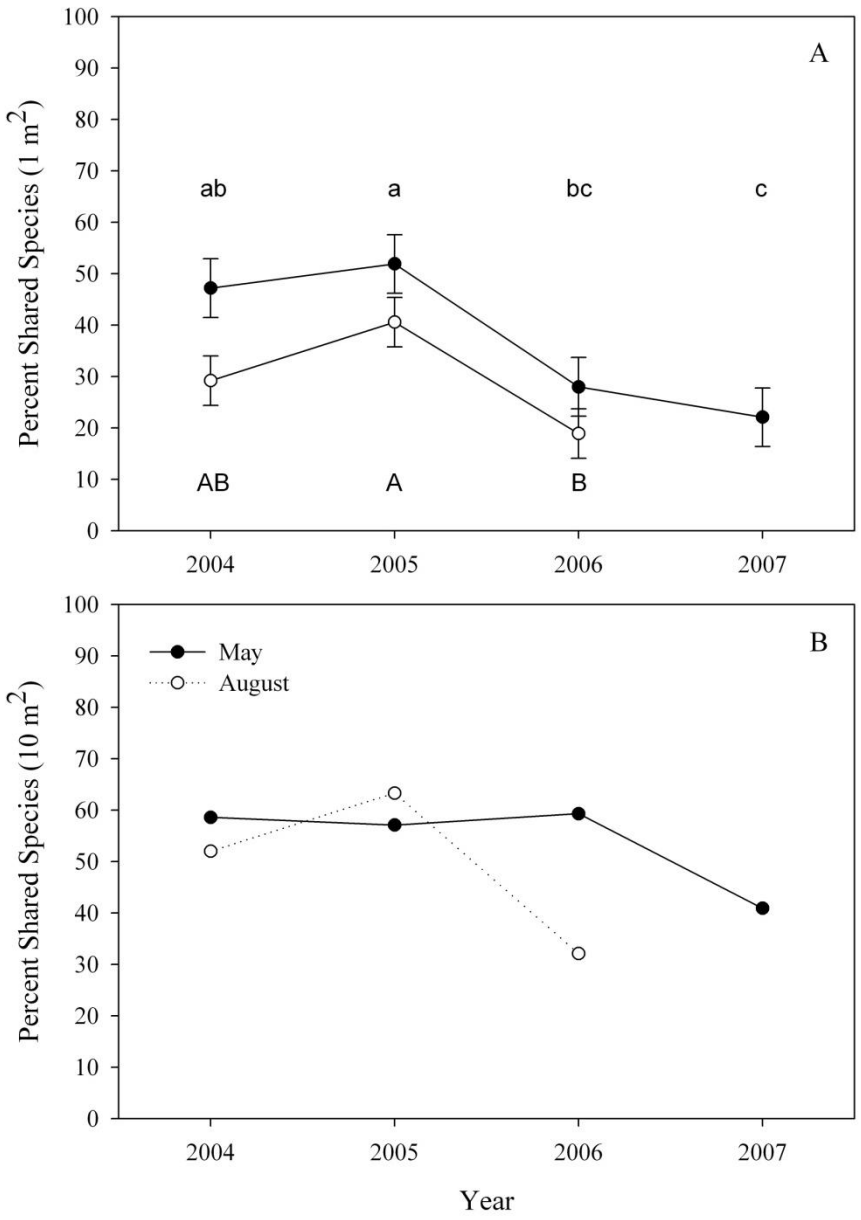

Fig. 3.3 – Average percentage of shared plant species in invaded and non-invaded community types at the per plot scale (1 m^2) (A) and totaled over all plots within a year (10 m^2) (B) for May and August. Years had significantly different ANOVA results for both May ($F = 6.52$; $P = 0.001$) and August ($F = 5.06$; $P = 0.01$) at the (1 m^2) level. Among year analyses were conducted using Tukey's HSD test. Different lower case letters indicate significantly different years for the May measurements. Different upper case letters indicate significantly different years for the August measurements ($\alpha=0.05$).

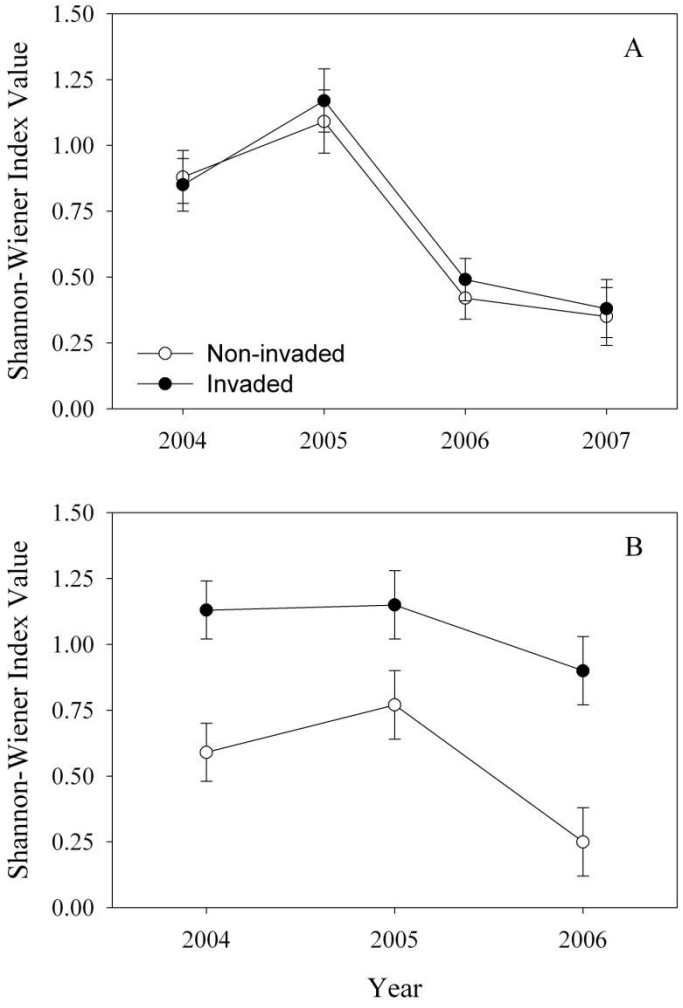

Fig. 3.4 – Average annual Shannon-Weiner index values for May (A) and August (B) measurements in invaded and non-invaded community types. Repeated measures MANOVA had a significant year effect in May ($F = 25.69$; $P < 0.001$) and significant community type ($F = 14.79$; $P = 0.001$) and year ($F = 16.34$; $P < 0.001$) main effects in August.

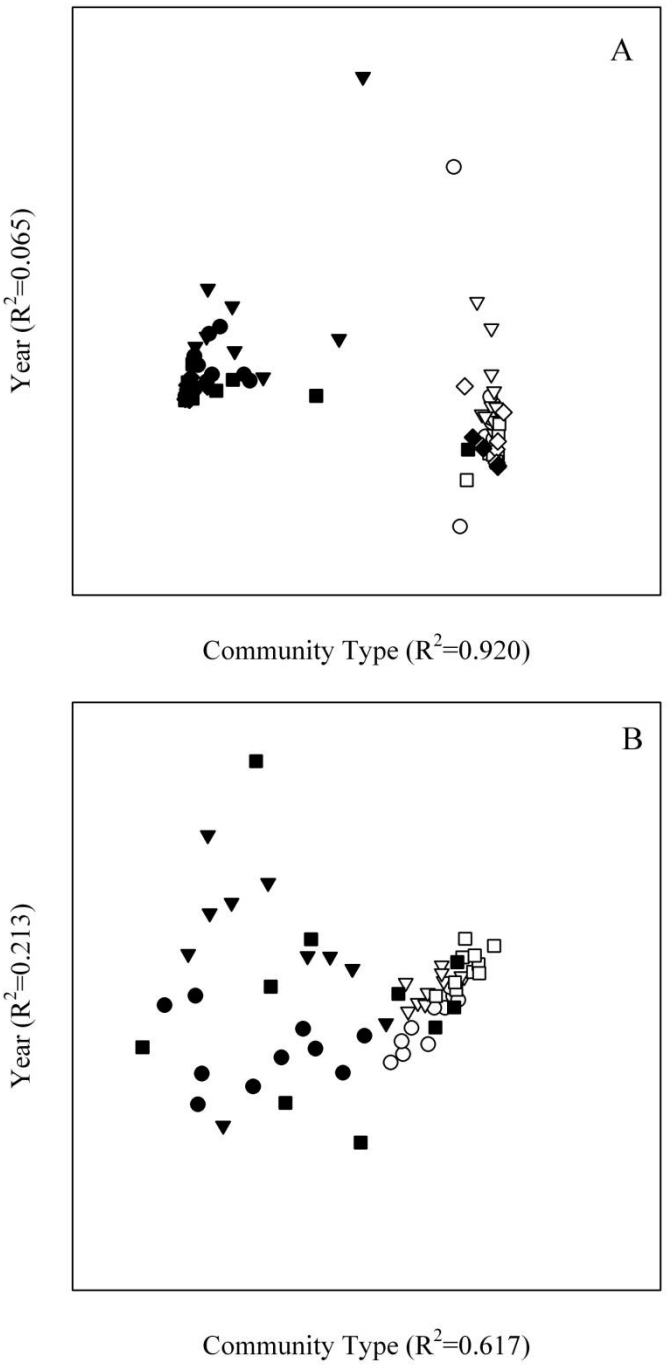

Fig. 3.5. NMS ordination for May (A) and August (B) measurements in non-invaded (white) and invaded (black) communities. Circles are 2004 measurements, triangles are 2005, squares are 2006, and diamonds are 2007 (exclusively for May). The final solution for the May NMS had two dimensions and represented 98.5% of the variation in the distance matrix (stress = 5.36; P = 0.02). The final solution for the August NMS had two dimensions and represented 83.0% of the variation in the distance matrix (stress = 13.59; P = 0.02).

Chapter 4
Mature native perennial grasses out-compete an invasive annual grass regardless of soil water and nutrient availability

Abstract

1. Competition and resource availability play an important role in regulating invasions of native perennial grass-dominated ecosystems by nonnative annual grasses such as *Bromus tectorum*.

2. We conducted two parallel greenhouse experiments examining the influence of six competition levels, high and low water availability and elevated N and P availability on growth of two native perennial grasses (*Elymus elymoides* and *Pascopyrum smithii*) and the invasive annual grass *B. tectorum*. We hypothesized that: 1) all three species would be negatively affected by increasing competition, 2) above- and belowground growth would increase with increased watering with *B. tectorum* having greater increases than the native perennial grasses and 3) above- and belowground growth would increase with N and P additions with *B. tectorum* having greater increases than the native perennial grasses.

3. *Bromus tectorum* growth was negatively affected by the presence of a single mature native perennial grass, regardless of species. The native perennial grasses were more influenced by intraspecific competition than by interspecific competition with *B. tectorum*. Increased water availability increased growth for all three species with no evidence for differential response by *B. tectorum*. N and P additions had few influences on growth.

4. *Synthesis*. Our study demonstrated that mature native perennial grasses such as *E. elymoides* and *P. smithii* are strong competitors against nonnative annual grasses such as

B. tectorum across differing water, N and P availability. This finding suggests that maintenance of intact perennial grass communities can reduce the risk of *B. tectorum* invasion even with temporal variations in resource availability.

Keywords

Bromus tectorum, Competition, *Elymus elymoides*, Greenhouse, Nitrogen, *Pascopyrum smithii*, Phosphorus, Water Availability

Introduction

Resource competition is an important driver of nonnative plant invasions. The ability of nonnative plants to establish and spread in new areas is highly dependent on their ability to acquire resources faster than, and often at the expense of, the native plants (Rees *et al.* 2001; Levine *et al.* 2003; Tilman 2004). Competitive differences between native and nonnative species depend on the taxa involved and environmental context in which the interactions occur because of species differences in growth and reproductive responses to resource availability (Rees *et al.* 2001). Understanding competitive interactions at the time of invasion can help guide prevention and post-invasion restoration efforts (Hobbs and Humphries 1995; Davis *et al.* 2000; D'Antonio and Meyerson 2002).

Bromus tectorum (cheatgrass) is an example of a highly competitive invasive nonnative species (Knapp 1996; Mack 1981). This Eurasian annual grass is the dominant species on ~20 million hectares of the Great Basin of the western U.S. and is found in all 48 contiguous states (Bradley and Mustard 2005; USDA, NRCS 2010). In areas where *B. tectorum* dominates, plant communities often have more frequent fire cycles (Whisenant 1990; D'Antonio and Vitousek 1992; Brooks *et al.* 2004) and altered biodiversity (Young and Evans 1978; Bolton *et al.* 1993; Brandt and Rickard 1994; Belnap and Phillips 2001). *Bromus tectorum* invasions are often driven by disturbance (Bradford and Lauenroth 2006), but undisturbed plant communities can also be invaded (Belnap and Phillips 2001; Evans *et al.* 2001). After invasion, *B. tectorum* can dominate an ecosystem for many decades (Brandt and Rickard 1994).

Competition with perennial grasses can restrict the spread of *B. tectorum*, and other nonnative annual grasses, into new areas (Yoder and Caldwell 2002; Booth *et al.* 2003; Chambers *et al.* 2007). The competitive ability of native perennial grasses against *B. tectorum* is highly dependent on the life stage of the perennial grasses. Greenhouse and field experiments have shown *B. tectorum* will generally out-compete perennial grass seedlings (Lowe *et al.* 2003; Humphrey and Schupp 2004). Evidence from field studies, however, suggests that mature perennial grasses, particularly *Elymus* sp. (squirreltail species) and species currently or formerly belonging to the genus *Agropyron* (wheatgrasses), can inhibit *B. tectorum* establishment and growth (Yoder and Caldwell 2002; Booth *et al.* 2003; Chambers *et al.* 2007).

As an annual grass, *B. tectorum* is more dependent on the immediate availability of essential resources than perennial grasses (Marschner 1995). The arid and semi-arid regions where *B. tectorum* has successfully invaded are, by definition, limited by water availability. Furthermore, nitrogen (N) availability can alter *B. tectorum* germination, growth, and competitive ability against perennial grasses (Blank *et al.* 1994; Lowe *et al.* 2003; Beckstead and Augspurger 2004). Availability of phosphorus (P) has been positively related to *B. tectorum* performance (Bashkin *et al.* 2003; Miller *et al.* 2006).

Recently, *B. tectorum* has established persistent populations in montane *Pinus ponderosa* (ponderosa pine) forests of northern Arizona (Laughlin and Fulé 2008; McGlone *et al.* 2009b). Field research has suggested that established perennial grasses and plant-available N and P may influence spatial patterns of *B. tectorum* invasion in Arizona pine forests. To evaluate the influence of competition and water and nutrient availability on *B. tectorum* and native perennial grass productivity, we conducted a

replacement series competition experiment in a greenhouse environment with *B. tectorum* seedlings and mature plants of two perennial grass species native to Arizona ponderosa pine forests: *Elymus elymoides* (bottlebrush squirreltail) and *Pascopyrum smithii* (western wheatgrass). The plants were grown at high and low water availability and with and without N and P amendments. We hypothesized that: 1) *B. tectorum* and native perennial grass growth would be negatively affected by interspecific competition, as would *B. tectorum* reproductive potential; 2) *B. tectorum* and native perennial grass growth would be positively affected by increased water availability, as would *B. tectorum* reproductive potential, but that *B. tectorum* would be more responsive to water additions than the perennial grass species and 3) *B. tectorum* and native perennial grass growth would be positively affected by nutrient amendments, as would *B. tectorum* reproductive potential, but that *B. tectorum* would be more responsive to nutrient amendments than the perennial grass species.

Materials and Methods

Experimental Design

This study was conducted at the Rocky Mountain Research Station Greenhouse in Flagstaff, AZ. We established two parallel replacement series experiments (de Wit 1960) each containing a native perennial grass in competition with *B. tectorum* in a 6 X 3 X 2 factorial randomized complete block design. For one experiment, we tested competition between *B. tectorum* and *E. elymoides*. The second experiment tested competition between *B. tectorum* and *P. smithii*. In each experiment, we tested the effects on plant production of six levels of interspecific competition, three levels of nutrient availability, and two levels of water availability; for *B. tectorum*, we also quantified floret and seed

production. All plants were grown in three-liter plastic pots in a medium of 75% soil mixed with 25% perlite to improve drainage. A plastic tray was set under each pot to minimize water loss and nutrient leaching. We collected soil for this project 10 km south of Flagstaff (35.1°N 111.69°W) in a ponderosa pine-dominated area with basalt-derived Typic Argiustolls of the Brolliar series. All three species used in the greenhouse experiment grow in the immediate vicinity of the soil collection area. Each of the 10 blocks contained one replicate of each treatment combination for a total of 720 pots. Each treatment replicate was assigned a random location within each block. The blocks were established along a moisture and temperature gradient starting at the cooling system on the south end of the greenhouse (wettest/coolest) and progressing to the ventilation fans at the north end of the greenhouse (hottest/driest).

Interspecific competitive ability (competition) was determined by comparing plant growth in species mixtures to growth in monocultures. The species mixtures were: 5/0, 4/1, 3/2, 2/3, 1/4, 0/5 native/*B. tectorum* plants. *Elymus elymoides* and *P. smithii* seeds were purchased from Granite Seed Company in Lehi, Utah. *B. tectorum* seed was collected in 2007 from *P. ponderosa* forests at Flagstaff and Mt. Trumbull, Arizona.

The water availability (water) factor consisted of two watering levels: high and low. Watering levels were based on soil moisture content measured in a *P. ponderosa*/bunchgrass community from field data collected near Flagstaff, approximately 2 km from our soil collection site. Soil moisture content ranged from an average of 4.3% immediately before the onset of summer monsoon rains in late June to 18.2% at the height of the rains in August. In the greenhouse, we monitored soil moisture (0 – 6 cm depth) using a HH2 moisture meter with an ML2x Theta probe (Delta-T Devices,

Cambridge, England). To avoid soil disturbances to the experimental pots resulting from inserting the moisture probe, we established an extra 10 high water and 10 low water pots (one each per block) for monitoring soil moisture. Each water-monitoring pot contained a monoculture of one of the species used in the experiment. We added 200 ml water to each pot when soil moisture content of the associated soil moisture-monitoring pots reached a lower threshold of 15% for the high water treatment and 5% in the low water treatment.

The nutrient availability (nutrient) factor included three levels: no fertilization, fertilization with ammonium nitrate (N treatment), or fertilization with Super Phosphate™ (P treatment). The N treatment was applied in aqueous solution on a biweekly basis and consisted of 7g N m^{-2} $year^{-1}$ applied eight times over the growing season. Lowe *et al.* (2003) reported increased performance in *B. tectorum* and *Bouteloua gracilis* (blue grama) seedlings with this level of N fertilization. Phosphorus was applied at a rate of 5g P m^{-2} $year^{-1}$ in a single application on April 1, 2008. This level has been shown to significantly increase aboveground growth in native perennial grasses in field studies in northern Arizona (G. Newman, School of Forestry, Northern Arizona University, *unpublished data*).

In May 2007 we planted the *E. elymoides* and *P. smithii* seeds at three times the desired density. After germination the seedlings were thinned to the target density. Soil moisture content was maintained above 10% during establishment. In August 2007, commensurate with the timing of field germination of *B. tectorum*, we planted the *B. tectorum* seeds at three times the target density and then thinned after germination. Locations of *B. tectorum* and native seeds within each pot were randomly assigned at

approximately equal distance from neighboring individuals and 3 cm from the pot edge. At the end of October 2007 we reduced the greenhouse temperature 3°C to induce dormancy. We applied an initial nutrient treatment of one-eighth the annual treatment (0.02g N per pot, or 0.88 g N m^{-2} and 0.01g P per pot, or 0.63 g P m^{-2}) prior to inducing dormancy. April 1, 2008, we increased the greenhouse temperature to a daytime maximum of 30°C and a nocturnal minimum of 18°C, and initiated the water and nutrient availability treatments. All measurements and harvests were completed in September at the end of the 2008 growing season.

We quantified aboveground biomass and number of leaves per plant for each species. We were unable to reliably separate roots by species, so we only measured total root biomass per pot. We also calculated root:shoot ratio pooled over species to assess the influence of treatments on biomass allocation. Additionally, we quantified *B. tectorum* reproduction based on per plant floret and seed production. We counted the number of leaves for each species and for *B. tectorum* we counted the number of florets on each plant in each pot during each three week sampling period. When *B. tectorum* had senesced in a pot we harvested all plants in that pot. When plants in the pots of all competition levels containing *B. tectorum* within a water-by-fertilizer combination within a block were harvested, plants in the pots of the monoculture of the native perennial grass for that treatment were also harvested. All aboveground biomass was clipped at the root crown then separated by species. To avoid damaging seeds we dried the biomass in a drying oven at 45°C for 96 hours. We weighed the biomass, separated the *B. tectorum* seeds from the biomass and counted the seeds. We calculated a per-plant average for all above-ground measurements. After completion of aboveground biomass harvests, we

harvested belowground biomass from all pots. Roots were separated by hand from the soil after soaking in a 1% hexametaphosphate solution. The biomass was then oven dried at 70°C for 48 hours and weighed.

Statistical Analysis

We used ANOVA to test for main effects and interaction effects of competition, water availability, and nutrient availability on each growth parameter for each species. The maximum temporal values recorded for number of leaves and *B. tectorum* florets per plant were used in the analyses. Species-level values of leaf count and aboveground biomass for each species as well as *B. tectorum* florets and seeds were averaged within pot to attain an average value per plant. We tested for normality and homogeneity using Shapiro-Wilk and Levene's tests, respectively. *Elymus elymoides* and *P. smithii* leaf count and aboveground biomass and whole pot root biomass and root:shoot ratio data met the assumptions for ANOVA. *Bromus tectorum* data on leaf count and aboveground biomass required log-transformation ($\ln(\chi+1)$). *Bromus tectorum* floret count and seed count required a cube root transformation. We conducted a post hoc Tukey's HSD analysis on all significant results except for the main effect of water which only had two levels of treatment and did not require post hoc analysis. Since leaf count and aboveground biomass can be highly correlated, we calculated a Pearson's correlation coefficient for each species to determine if both variables should be analyzed or if one is an adequate description of aboveground productivity. All analyses were conducted using JMP software (version 8.0, SAS Institute 2008).

Results

Number of leaves and aboveground biomass were positively and highly correlated for all three species. For *B. tectorum*, number of leaves and aboveground biomass had correlation coefficients of r = 0.84 when grown in competition with *E. elymoides* and r = 0.85 when grown with *P. smithii*. *Elymus elymoides* had a correlation coefficient of r = 0.82 and *P. smithii* had a coefficient of r = 0.89 over all treatments. Due to these high correlation coefficients, we elected to only report data on aboveground biomass for each species.

The role of competition

The main effect of competition was consistently significant for all response variables tested for every species (Tables 4.1 and 4.2). Every measure of *B. tectorum* performance per plant was significantly reduced when grown with one or more mature individuals of native perennial grasses (Figs 4.1 and 4.2). The presence of a single mature *E. elymoides* plant reduced aboveground biomass and floret count of *B. tectorum* by a minimum of 74% (Fig. 4.1). Subsequent reductions in *B. tectorum* performance with increasing numbers of *E. elymoides* were typically < 50%, with small changes in absolute values of aboveground biomass and floret production (Fig. 4.1). *Bromus tectorum* seed production had a significant competition x nutrient interaction (Table 4.1), but seed production was greater in the *B. tectorum* monoculture than in competition with *E. elymoides* regardless of nutrient availability (Fig. 4.1B). The competition x water and competition x nutrient interactions were significant for floret production, but in both instances per-plant floret production was significantly greater in the *B. tectorum*

monoculture than in competition with *E. elymoides* regardless of water or nutrient availability (Fig. 4.1C,D).

The same trends for *B. tectorum* performance detected in competition with *E. elymoides* were also detected in competition with *P. smithii*, with a reduction in *B. tectorum* performance by at least 72% in the presence of one native perennial grass (Fig. 4.2). As with *E. elymoides*, subsequent additions of *P. smithii* had less impact on *B. tectorum* aboveground biomass, seed production, and floret production (Fig. 4.2). *Bromus tectorum* floret production had a significant three-way competition x water x nutrient interaction (Table 4.2) because of uneven effects of water and nutrient additions over levels of competition (Fig. 4.2B). Despite this interaction, *B. tectorum* floret production per plant was greater in *B. tectorum* monoculture than at all levels of competition, regardless of water and nutrient availability (Fig. 4.2B).

The main effect of competition was significant for aboveground biomass production per plant of both native perennial grasses (Tables 4.1 and 4.2). In every case, growth was lowest in the native grass monocultures and progressively increased with increased presence of *B. tectorum* (Figs 4.3 and 4.4).

The competition main effect was significant for root production and root:shoot ratio for both the *B. tectorum – E. elymoides* and the *B. tectorum – P. smithii* experiments (Tables 4.1 and 4.2). For root biomass, the *B. tectorum* monoculture always had the lowest biomass and the native perennial grasses had the greatest, with the combination of species having intermediate values (Figs 4.5A and 4.6A). The *B. tectorum* monoculture in both experiments had an approximately 1:1 root:shoot ratio, while the native perennial

grass monocultures had significantly higher ratios (Figs 4.5C and 4.6B). The pots with a species mixture had intermediate values.

The Role of Water Availability

Water availability significantly affected *B. tectorum* production in the *E. elymoides* experiment (Table 4.1). Per-plant aboveground biomass was greater in the high water treatment (0.81 g dry weight ± 0.09 [mean ± standard error]) than in the low water treatment (0.60 g dry weight ± 0.09). Seed production per plant was also greater in the high water treatment (58.73 seeds ± 4.21) than in the low water treatment (20.81 seeds ± 4.49). The competition x water interaction was a significant influence on *B. tectorum* floret production (Table 4.1) because the increase in floret production by watering was slightly uneven over competition levels (Fig. 4.1C).

When grown in competition with *P. smithii*, the water main effect was significant for *B. tectorum* aboveground biomass, seed production, and floret production (Table 4.2). *Bromus tectorum* per-plant aboveground biomass was greater in the high water treatment (0.71 g dry weight ± 0.09) than in the low water treatment (0.60 g dry weight ± 0.09). There was a significant water x nutrient interaction for seed production, although seed production was always greater in the high water treatment regardless of nutrient amendment (Fig. 4.2D). There was a significant competition x water x nutrient interaction for floret production (Table 4.2) due to uneven effects of both N and P additions over competition levels. For most competition levels and nutrient availabilities the high water availability treatments had greater floret production (Fig. 4.2B).

There was a significant water main effect for *E. elymoides* aboveground biomass (Table 4.1). Per-plant aboveground biomass was greater in the high water availability

treatment (4.66 g dry weight ± 0.28) than in the low water treatment (3.74 g dry weight ± 0.28). *Pascopyrum smithii* showed a significant water main effect for aboveground biomass (Table 4.2). Per-plant aboveground biomass was greater in the high water treatment (4.53 g dry weight ± 0.21) than in the low water treatment (3.27 g dry weight ± 0.21).

Root biomass production and root:shoot ratio were responsive to changes in water availability (Tables 4.1 and 4.2). The *B. tectorum – E. elymoides* experiment had a significant water x nutrient interaction, but the main effect of water availability was not significant (Table 4.1). Water and the water x competition interaction were significant sources of variation in root biomass production in the *B. tectorum – P. smithii* experiment (Table 4.2). Root biomass was consistently greater in the high water pots except for the *B. tectorum* monoculture treatment in which the high water treatment had the lowest root biomass of all competition x water treatment combinations (Fig. 4.6A). There was a significant water main effect for root:shoot ratio in the *B. tectorum – E. elymoides* experiment (Table 4.1), with a higher root: shoot ratio in the low water treatments (High 1.22 ± 0.05; Low 1.60 ± 0.05). There were no significant root:shoot ratio responses to water availability in the *B. tectorum – P. smithii* experiment (Table 4.2).

The Role of Nutrient Availability

None of the species in this experiment showed a significant response to the main effect of nutrient availability for any of the response variables we measured (Tables 4.1 and 4.2). The only detectible influence of nutrients in our study was for *B. tectorum* floret and seed production in both native perennial grasses competition experiments, and root biomass production for the *B. tectorum – E. elymoides* experiment (Tables 4.1 and 4.2).

In the *B. tectorum – E. elymoides* experiment, the competition x nutrient interaction was significant for *B. tectorum* floret production (Table 4.1) due to uneven effects of nutrient additions over competition levels (Fig. 4.1D). Our interpretation of this interaction was that N addition stimulated floret production most when *B. tectorum* competed with four *E. elymoides* plants. In competition with *P. smithii* there was a significant competition x water x nutrient interaction in *B. tectorum* florets per plant (Table 4.2). This interaction was largely due to stimulation of floret production by N additions in the high water treatment when *B. tectorum* was grown in competition with wheatgrass (Fig. 4.2B). The *B. tectorum – E. elymoides* experiment had a significant competition x nutrient interaction for seed production (Table 4.1). *Bromus tectorum* seed production was generally lowest in the N amendments, except for the four *E. elymoides* to one *B. tectorum* competition level in which the N amendment had the greatest seed production (Fig. 4.1B). The *B. tectorum – P. smithii* experiment had a significant water x nutrient interaction for *B. tectorum* seed production (Table 4.2) due to stimulation of seed production in the high water high N combination, but lowest seed production in the low water high N combination (Fig. 4.2D). Root biomass production for the *B. tectorum – E. elymoides* experiment had a significant water x nutrient availability interaction (Table 4.1) due to stimulation of biomass by watering only at high N availability (Fig. 4.5B).

For most of the significant nutrient interactions for all species, P addition had intermediate values for seed and floret production when compared to the control and N addition. There were a few exceptions, however. In the *E. elymoides* experiment, *B. tectorum* seed count was highest with P addition in two of the competition levels and *B. tectorum* floret production was highest with P addition at one of the competition levels

(Fig. 4.1B,D). *Bromus tectorum* seed count in the *P. smithii* experiment was higher with P addition at low water availability than with the N addition or control at low water (Fig. 4.2D).

Discussion

The Role of Competition

Both *B. tectorum* and perennial grass individuals were strongly influenced by interspecific competition, though with opposite responses. *Bromus tectorum* response to competition was consistent with our first hypothesis that production would be negatively influenced by the presence of mature perennial grasses. Although *B. tectorum* production varied with increasing numbers of perennial grasses, the greatest change occurred in the presence of a single mature perennial grass. Perennial grass production was influenced by *B. tectorum*, but the response was opposite of our hypothesis, with per-plant production of the mature perennial grasses increasing with increasing presence of *B. tectorum* and with reduced intraspecific competition.

Our study demonstrates that mature perennial grasses can be strong competitors with nonnative annual grasses. This suggests that the presence of a robust native perennial grass community may mitigate the likelihood and intensity of nonnative annual grass invasions. There is supportive evidence for this interpretation in field studies. In Utah, *B. tectorum* competition had little negative influence on two-year-old *E. elymoides* plants growing in *B. tectorum*-dominated areas (Humphrey and Schupp 2004). Leger (2008) showed that *Elymus multisetis* (big squirreltail) plants that persisted in *B. tectorum*-dominated areas were more competitive against *B. tectorum* than conspecific plants growing in non-invaded areas, and suggested that genotypic selection occurred

after invasion. In a Great Basin study, there was a positive relationship between native perennial plant removal and *B. tectorum* biomass per plant (Chambers *et al.* 2007). Additionally, there was a positive relationship between *Agropyron cristatum* (crested wheatgrass) removal and *B. tectorum* biomass per plant, as well as number of seeds produced per *B. tectorum* plant. Booth *et al.* (2003) showed that areas with > 20% cover of *E. elymoides* cover had little or no *B. tectorum*. There have been instances, however, when an intact perennial grassland was not able to successfully exclude nonnative annual grass invasion. In Canyonlands National Park, *B. tectorum* invaded a perennial grassland dominated by *Achnatherum hymenoides* (Indian ricegrass) and *Pleuraphis jamesii* (James' galleta) (Belnap and Phillips 2001; Evans *et al.* 2001). *Bromus tectorum* was able to invade this system in spite of the presence of mature perennial grasses and there is some evidence that *P. jamesii* actually facilitates *B. tectorum* biomass production by ameliorating nutrient constraints in the soil (Belnap and Sherrod 2009). In a Mohave Desert field study, mature *A. hymenoides* and *Pleuraphis rigida* (big galleta) had reduced relative growth rates with increasing competition from *Bromus rubens* (red brome) (DeFalco *et al.* 2007). These results suggest that competitive relationships between nonnative annual and native perennial grasses are species-specific and not applicable at the functional group level.

In contrast to the results of our study, competition between nonnative annual grasses and native perennial grass seedlings typically favors the annual species. In the above-mentioned Utah study, *B. tectorum* competition had a strong negative influence on *E. elymoides* seedlings (Humphrey and Schupp 2004). In a seedling competition study, increasing density of *Taeniatherum caput-medusae* (medusahead*)* significantly decreased

E. elymoides biomass, while *E. elymoides* density had no influence on *T. caput-medusae* biomass (Young and Mangold 2008). Seedlings from native *Sporobolus airoides* (alkali sacaton) had significantly reduced growth and survival in competition with *Bromus diandrus* (ripgut brome) and *Hordeum marinum* spp. *gussoneanum* (Mediterranean barley) (Hoopes and Hall 2002). The inability of native perennial grass seedlings to compete with nonnative annual grasses suggests that disturbances that reduce perennial grasses can leave the community highly vulnerable to invasion.

Intraspecific competition appears to be an important regulator of performance for both *E. elymoides* and *P. smithii*, but not *B. tectorum*. This may be the result of higher belowground biomass production in the native perennial grasses than *B. tectorum*. Monaco *et al.* (2003) reported lower root:shoot ratios for *B. tectorum* and *T. caput-medusae* than for *E. elymoides, E. multisetis*, and *Pseudoroegneria spicata* (bluebunch wheatgrass). Interestingly, unlike the results of this study, in the Monaco *et al.* (2003) study, *B. tectorum* monocultures had comparable belowground biomass to that of the three native perennial grasses. *Taeniatherum caput-medusae*, however, had lower belowground biomass than the perennial grasses. Greater root production by perennial grasses should give them a competitive advantage over *B. tectorum* or other annual grasses with less extensive root systems (Cline *et al.* 1977). This disparity in root biomass between perennial and annual grasses would likely be less pronounced in perennial grass seedlings (Arredondo *et al.* 1998), potentially explaining the differences in the competitive ability of perennial grasses at different life stages.

The Role of Water Availability

Water is an important limiting resource in most areas where *B. tectorum* has heavily invaded, including northern Arizona ponderosa pine forests. It is therefore not surprising that all three species responded positively to water amendments, consistent with our second hypothesis. Contrary to this hypothesis, however, there was little evidence that *B. tectorum* was more responsive to water amendments, with all three species having approximately 20 – 40% increases in aboveground biomass with increased water availability. Furthermore, the only competition–by-water availability interaction for any measure of biomass production was detected in root biomass in the *B. tectorum – P. smithii* experiment, with significant responses to increased water availability only observed in the species combinations with zero or one *B. tectorum* individual (Fig. 4.6A). This is surprising because moisture availability, particularly in association with N availability, has been associated with *B. tectorum* growth and invasion success (Cline and Rickard 1973; Link *et al.* 1995). Also, competition for water with *B. tectorum* has been shown to negatively affect the native perennial grass *Hesperostipa comata* (needle and thread*)* water status and productivity (Melgoza *et al.* 1990). Beckstead and Augspurger (2004), however, showed no significant response in *B. tectorum* biomass or density from water additions in mixed communities of *B. tectorum*, *Poa secunda* (Sandberg bluegrass), and *E. elymoides* unless the water additions were combined with N additions and removal of neighboring plants.

It is likely that the timing of precipitation, not the general availability of water, is most important for *B. tectorum* performance. Miller *et al.* (2006) detected significantly greater *B. tectorum* fall seedling establishment, mid-spring relative growth rates, and final

biomass in plots with high water availability when compared to plots with low water. Early spring growth rates were actually greater in the low water plots than with high water (Miller *et al.* 2006). At other growth stages, high water availability did not influence growth. High levels of precipitation during the germination period for *B. tectorum* have been associated with past invasions (Belnap and Phillips 2001; Evans *et al.* 2001, McGlone *et al.* 2009a). Furthermore, the success of *B. tectorum* and other annual nonnative bromes in competing with native perennial grasses has been attributed to the earlier physiological activity of annual bromes in the growing season, and therefore earlier access to water resources (Knapp 1996; DeFalco *et al.* 2007). *Elymus elymoides* is also physiologically active early in the growing season which may account for its ability to successfully compete with *B. tectorum* (Booth *et al.* 2003).

The Role of Nutrient Availability

Surprisingly, our data do not support our third hypothesis that N and P additions would have a greater influence on *B. tectorum* growth than the native perennial grasses. In fact, N and P had little overall influence on the performance of *B. tectorum* or the native perennial grasses with the exception of *B. tectorum* floret and seed production. Interestingly, average seed production for *B. tectorum* was always above parental replacement value (i.e. – one viable seed per plant), regardless of competition or resource levels. Plant-available N and P are considered the most commonly limiting nutrients in most ecosystems (Elser *et al.* 2007). Past research has shown N and/or P additions to have a positive effect on *B. tectorum* performance (Lowe *et al.* 2003; Beckstead and Augspurger 2004; Miller *et al.* 2006). In a replacement series competition study between *B. tectorum* and *Bouteloua gracilis* seedlings, the addition of 1 g N m^{-2} increased *B.*

tectorum biomass and the addition of 4 g N m^{-2} reduced *B. gracilis* biomass in competition with *B. tectorum* (Lowe *et al.* 2003).

Nonnative annual grasses often show greater growth responses to N and P additions than native perennial grasses. With N fertilization, *B. tectorum* and *T. caput-medusae* had greater NO_3 uptake and shoot production when compared to *E. elymoides*, *E. multisetis*, and *P. spicata* (Monaco *et al.* 2003). The addition of N at lower rates (5 g N m^{-2}) than used in this study caused a seven-fold increase in *Schismus arabicus* (Arabian schismus) biomass in the Mojave Desert, while P additions at the same rate as this study caused a 40% increase in *S. arabicus* biomass (Williams and Bell 1981). With *B. rubens* and *S. arabicus*, Brooks (2003) detected significant increases in density and biomass with additions of 3.2 g N m^{-2} $year^{-1}$, a rate of atmospheric N deposition similar to near-urban areas of the Mojave Desert.

The lack of growth response to nutrient additions in this study suggests that neither N nor P was a single limiting resource. Since competition had a significant effect on growth performance of all three species, this gives rise to the question: for what resource were the plants differentially competing? We suggest four possible answers: 1) that water remained limiting, even in the high water treatment, 2) N and P were co-limiting, 3) either N or P was limiting, but co-limiting with another nutrient or 4) a nutrient not tested in this experiment limited biomass production.

Conclusions

Interactions between invasive plant species and indigenous species are complex and can vary depending on the species involved, species' life history, resources that are currently limiting growth, soil properties, and numerous other variables. Our study and

several others suggest that mature native perennial grasses of montane forests of the western U.S., such as *E. elymoides* and *P. smithii*, are often strong competitors against invasive annual grasses, such as *B. tectorum*. Moreover, the competitive dominance of these mature perennial grasses over *B. tectorum* was maintained at both low and high availabilities of soil water, nitrogen, and phosphorus. Our results suggest robust mature native perennial grasses are more important detriments to *B. tectorum* invasion of montane forests of the western U.S. than short-term variations in soil resources.

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Table 4.1 – Significant ANOVA results for the *B. tectorum – E. elymoides* competition experiment

Species	Source	F Statistic	P Value
B. tectorum			
	Aboveground Biomass per Plant		
	Competition	187.40	<0.001
	Water	32.15	<0.001
	Floret Production per Plant		
	Competition	72.55	<0.001
	Water	49.53	<0.001
	Competition x Water	3.15	0.02
	Competition x Nutrient	1.99	0.05
	Seed Production per Plant		
	Competition	16.17	<0.001
	Water	64.92	<0.001
	Competition x Nutrient	2.14	0.03
E. elymoides			
	Aboveground Biomass per Plant		
	Competition	85.73	<0.001
	Water	12.90	<0.001
Pooled			
	Root Biomass		
	Competition	2.98	0.01
	Water x Nutrient	4.46	0.01
	Root:shoot Ratio		
	Competition	5.52	<0.001
	Water	28.42	<0.001

Table 4.2 – Significant ANOVA results for the *B. tectorum – P. smithii* competition experiment

Species	Source	F Statistic	P Value
B. tectorum			
	Aboveground Biomass per Plant		
	Competition	190.51	<0.001
	Water	5.20	0.02
	# Florets per Plant		
	Competition	88.67	<0.001
	Water	16.61	<0.001
	Competition x Water x Nutrient	2.04	0.04
	Seed Production per Plant		
	Competition	28.07	<0.001
	Water	32.16	<0.001
	Water x Nutrient	3.95	0.02
P. smithii			
	Aboveground Biomass per Plant		
	Competition	51.14	<0.001
	Water	17.33	<0.001
Pooled			
	Root Biomass		
	Competition	9.92	<0.001
	Water	35.34	<0.001
	Competition x Water	2.62	0.02
	Root:shoot ratio		
	Competition	19.78	<0.001

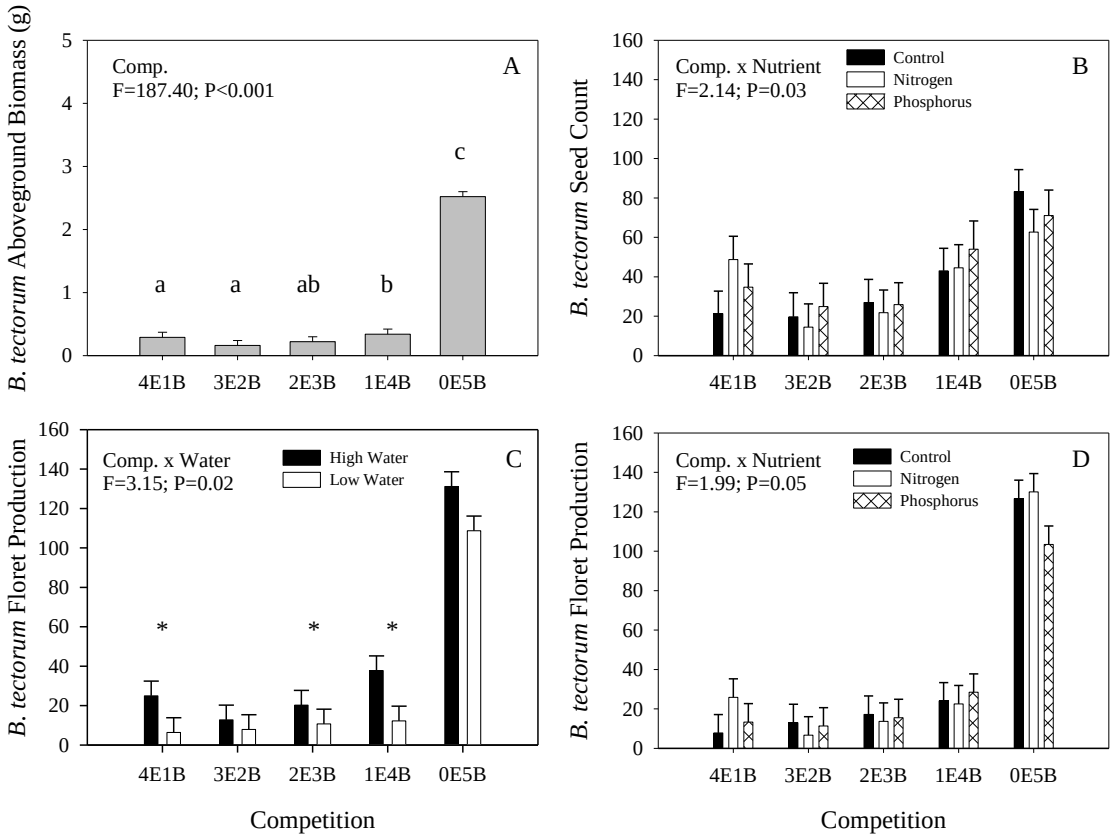

Fig. 4.1 - *Bromus tectorum – E. elymoides* competition experiment significant results for *B. tectorum* aboveground biomass per plant (A), *B. tectorum* seed production per plant (B), and *B. tectorum* floret production per plant (C, D). Species composition codes = # *E. elymoides* # *B. tectorum*, thus 4E1B = 4 *E. elymoides* 1 *B. tectorum*. Significant ANOVA results are shown in upper left corner of each graph. Different letters in panel A denote significantly different Tukey's HSD results. Asterisks in panel C denote significant differences between water treatments, within competition levels, 0E5B competition level was significantly different than the other competition levels (α=0.05). Post hoc results are not shown for panels B & C for clarity of presentation, but are discussed in the text. Analyses were conducted on transformed data. Nontransformed data are presented in graphs.

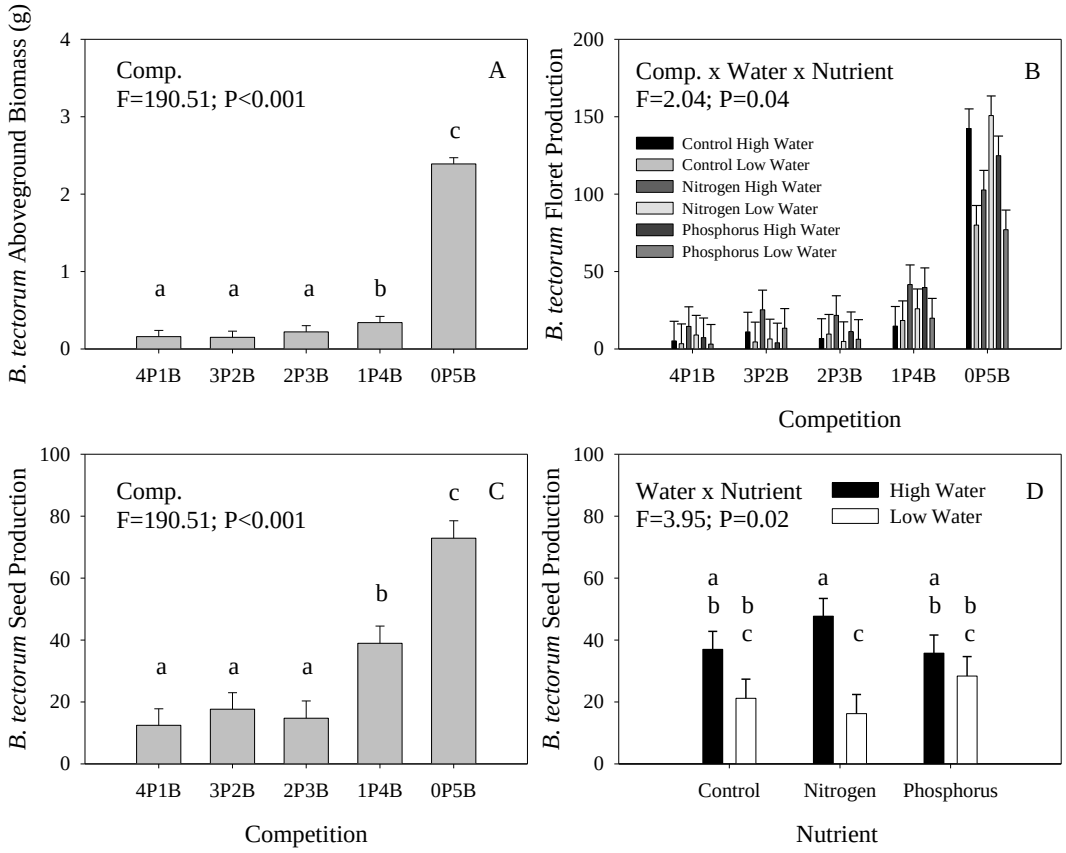

Fig. 4.2 - *Bromus tectorum – P. smithii* competition experiment significant results for *B. tectorum* aboveground biomass per plant (A), *B. tectorum* florets per plant (B), and *B. tectorum* seed production per plant (C, D). Species composition codes = # *P. smithii* # *B. tectorum*, thus 4P1B = 4 *P. smithii* 1 *B. tectorum*. ANOVA results are shown in upper left corner of each graph. Different letters in panels A, C & D denote significantly different Tukey's HSD results (α=0.05). Post hoc results are not shown for panel B for clarity of presentation, but are discussed in the text. Analyses were conducted on transformed data. Non-transformed data presented in graphs.

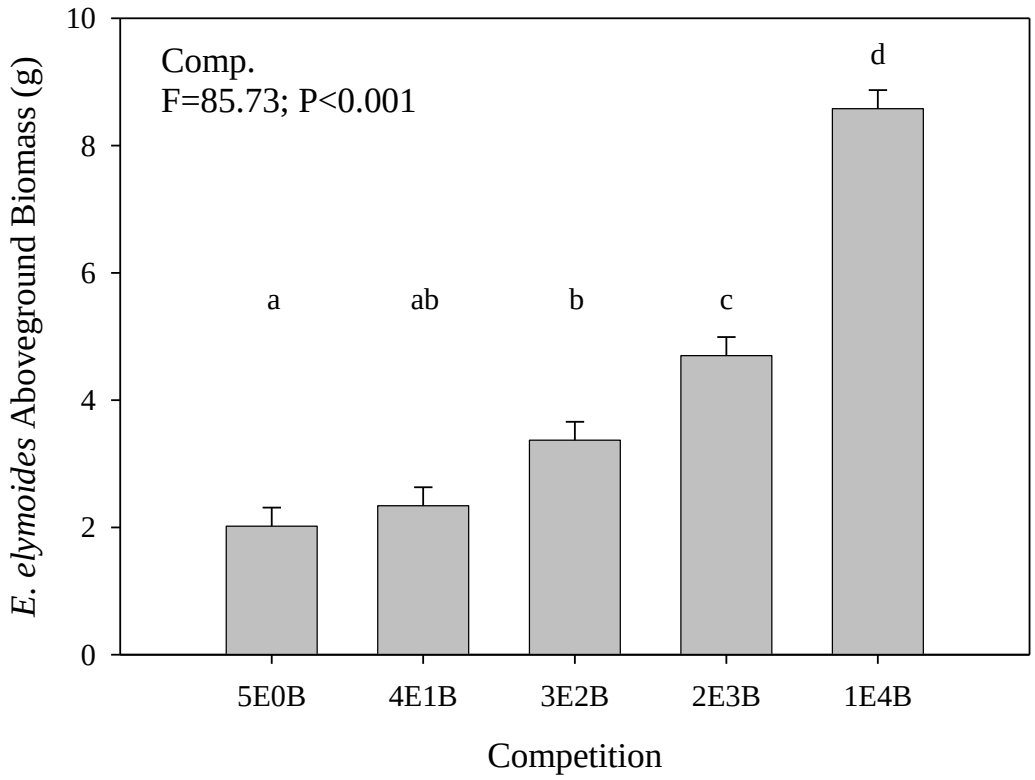

Fig. 4.3 - *Bromus tectorum – E. elymoides* competition experiment significant results for *E. elymoides* aboveground biomass per plant. Species competition codes = # *E. elymoides* # *B. tectorum*, thus 4E1B = 4 *E. elymoides* 1 *B. tectorum*. ANOVA results are shown in upper left corner of the graph. Different letters denote significantly different Tukey's HSD results (α=0.05).

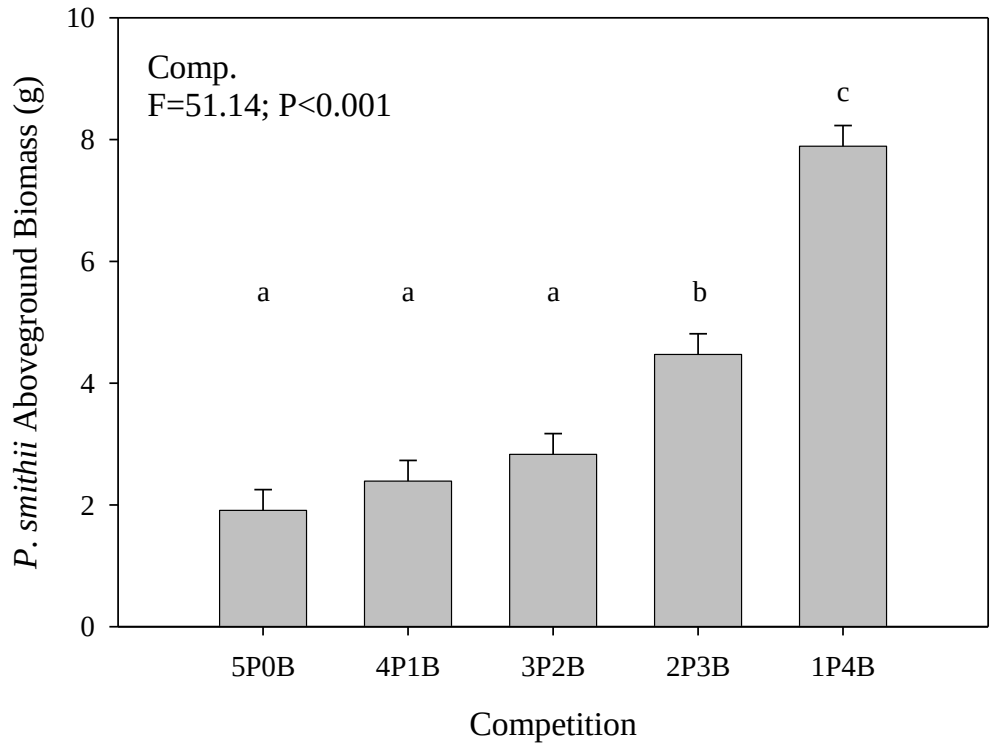

Fig. 4.4 - *Bromus tectorum – P. smithii* competition experiment significant results for *P. smithii* biomass per plant. Species competition codes = # *P. smithii* # *B. tectorum*, thus 4P1B = 4 *P. smithii* 1 *B. tectorum*. ANOVA results are shown in upper left corner of the graph. Different letters denote significantly different Tukey's HSD results (α=0.05).

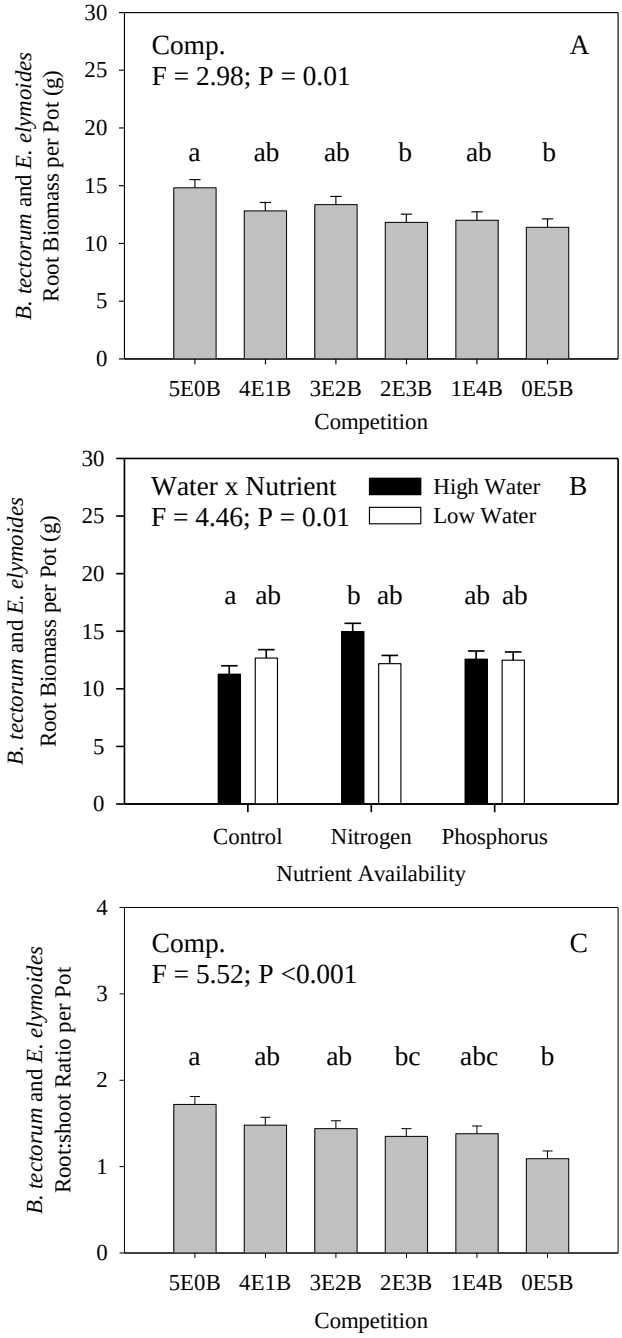

Fig. 4.5 - *Bromus tectorum – E. elymoides* competition experiment significant results for total root biomass per pot (A, B) and root:shoot ratio per pot (C). Species competition codes = # *E. elymoides* # *B. tectorum*, thus 4E1B = 4 *E. elymoides* 1 *B. tectorum*. ANOVA results are shown in upper left corner of each graph. Different letters denote significantly different Tukey's HSD results (α=0.05).

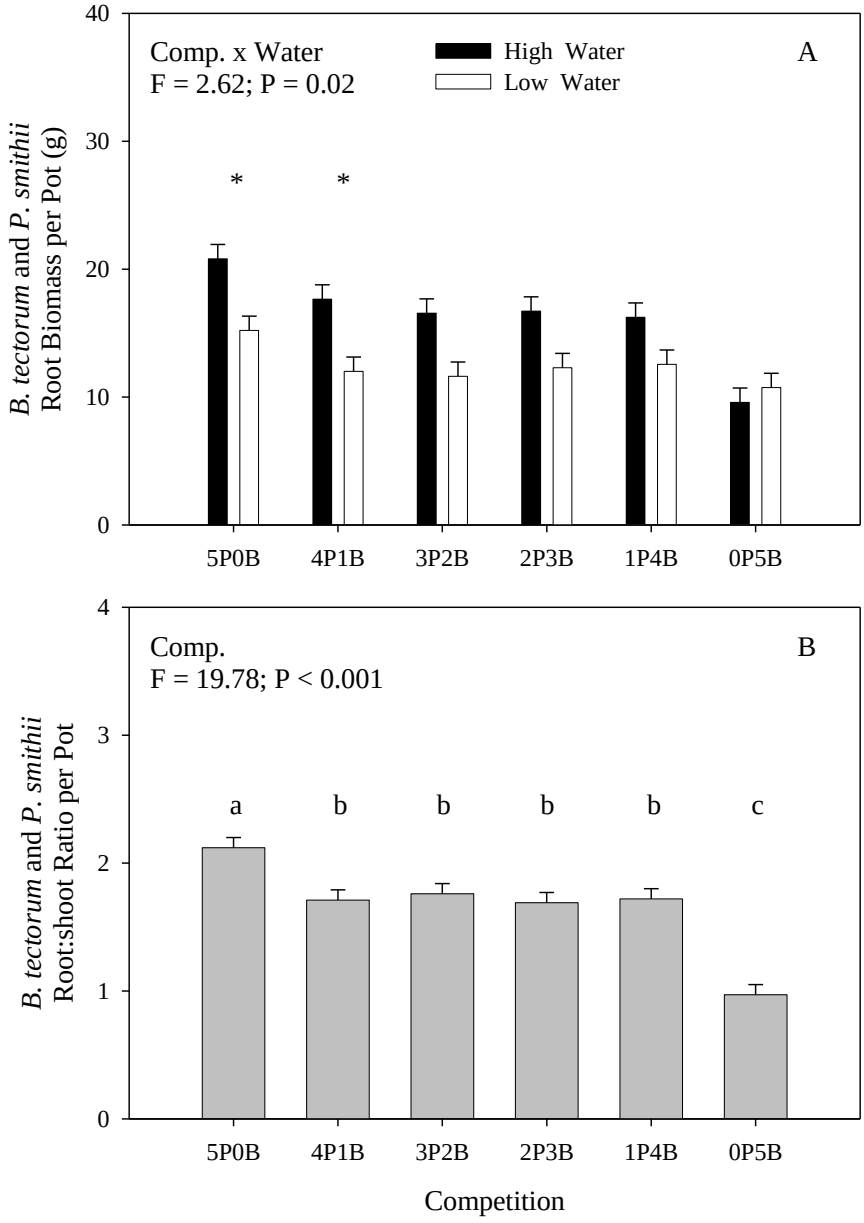

Fig. 4.6 - *Bromus tectorum – P. smithii* competition experiment significant results for total root biomass per pot (A) and root:shoot ratio per pot (B). Species composition codes = # *P. smithii* # *B. tectorum*, thus 4P1B = 4 *P. smithii* 1 *B. tectorum*. ANOVA results are shown in upper left corner of each graph. Asterisks in panel A denote significantly different results between water treatments, within competition levels. Different letters in panel B denote significantly different Tukey's HSD results (α=0.05).

Chapter 5
Management Implications

Prevention and control of nonnative plant invasions pose an increasingly difficult challenge to land managers. Despite an intense amount of current research on invasion ecology, we still have limited ability to predict invasions and even less understanding of how to reverse invasions. Methods for reducing invasion intensity have included mowing, targeted grazing, biocontrol, herbicide application, seeding, and soil nutrient manipulation (Rinella et al., 2010, Diamond et al., 2009, Davison and Smith, 2007, Corbin and D'Antonio, 2004, Cox and Anderson, 2004, Reever Morghan and Seastedt, 1999, Hull Jr. and Stewart, 1948). To date, successes have been rare while the spread of nonnatives continues to occur at a rapid pace. The potential changes imposed on the ecosystem by invasion does, however, warrant continued effort to prevent or mitigate future invasions. Community domination by a nonnative plant species can lead to changes in biodiversity, altered disturbance regimes, and altered soil nutrient cycling (Brooks et al., 2004, Evans et al., 2001, Mack et al., 2000, Parker et al., 1999, D'Antonio and Vitousek, 1992). These changes are generally regarded as undesirable and most public land management agencies include control of nonnative species as one of their management objectives.

This study adds to an increasing body of research highlighting the importance of preserving and maintaining the native vegetation community, particularly perennial grasses, in mitigating annual grass invasion (Chapters 2 & 3). Robust populations of bottlebrush squirreltail (*Elymus elymoides*), various species of wheatgrass (*Agropyron* sp.), and other perennial grasses have been shown to effectively exclude nonnative annual

grass encroachment in several ecosystems (Chambers et al., 2007, Cox and Anderson, 2004, Booth et al., 2003). This suggests the need to minimize disturbance to the extant perennial grass community. Minimizing such disturbances poses a significant challenge to land managers, since many public land policies mandate activities that disturb understory vegetation. Grazing, off-road vehicle use, and logging can damage vegetation and disturb soil. Land management practices designed to promote ecosystem restoration can also generate disturbances that can compromise the plant community, at least in the short term. Many forest restoration practices involve tree or shrub removal to promote growth of perennial grasses and other herbaceous plants. Woody plant removal at large scales generally requires the use of heavy machinery that can severely disturb the soil and understory vegetation. Forest restoration can also involve the reinstatement of natural disturbances such as fire and flooding. While these disturbances can stimulate soil nutrient cycling, remove accumulated plant litter, and prevent canopy closure by removing aboveground biomass of woody species, the disturbances can also harm extant perennial grasses, creating potential habitat for nonnative plant species encroachment.

Many degraded ecosystems lack a substantial community of native perennial grasses. The absence of a robust herbaceous plant community is an important criterion for identifying areas in need of ecological restoration or changes in the traditional land management practices on that site (Allen et al., 2002, Moore et al., 1999). Establishing perennial grasses may require proactively increasing propagule levels of desired species. This is typically accomplished through seeding. In our field study, seeding of three native perennial plant species failed to elicit a detectable response (Chapter 2). All of the increases in seeded species occurred through natural recruitment. An increasing number

of studies have shown seeding to have limited success in promoting rapid establishment of native species. Furthermore, there is increasing concern that seeded projects have inadvertently spread nonnative seeds through contaminated seed mixes (Keeley et al., 2006). This suggests that alternative methods must be explored for propagating desired species in disturbed areas. Possible options include planting established individuals from nearby areas or seeding with early successional species that have high germination rates and can establish quickly. Some researchers have advocated "assisted succession" through seeding nonnative perennial grasses to minimize nonnative annual grass encroachment (Cox and Anderson, 2004). The nonnative perennial grasses would stabilize the soil, create a perennial species-dominated community, and allow managers to encourage native species to establish. This approach has been met with skepticism, however, since seeding nonnative species is often contrary to the objectives of land management projects and on some public lands is not allowed. Furthermore, there is limited evidence that areas seeded with nonnative perennial grasses will eventually convert to native-dominated communities and there are many examples of seeded nonnative perennial grasses being highly resistant to the reestablishment of native species.

Cheatgrass (*Bromus tectorum*) is a highly persistent invader and attempts to remediate cheatgrass-dominated areas have generally been unsuccessful. Researchers have tried herbicide, targeted grazing, biocontrol with fungi, seeding, mowing, and soil nutrient depletion with carbon amendments (Dooley and Beckstead, 2010, Baker et al., 2009, Diamond et al., 2009, Meyer et al., 2007, Belnap et al., 2003). While many of these techniques generate a short-term reduction in cheatgrass abundance, none have reliably

shifted the community back to a native-dominated plant community. This suggests that a multifaceted approach would be necessary to eliminate cheatgrass dominance in invaded areas. It is insufficient to simply reduce cheatgrass abundance. The native plant community must also be proactively enhanced, particularly with species that are highly competitive with cheatgrass such as bottlebrush squirreltail (Chapter 4). As stated above, it can be very difficult to rapidly establish native perennial species through seeding and it may be necessary to plant established individuals of desired species. This would likely require a source of plants that is reasonably close to the planting site. Furthermore, post-planting maintenance such as watering and grazing exclusion may be necessary to ensure successful establishment of the native plants. While this would be more labor-intensive than current seeding programs, the general lack of success with seeding warrants the exploration of other mechanisms of native plant reestablishment.

Funding and resources for land management are always limited, requiring practitioners to prioritize for the most effective use of available resources. To accomplish this, it will likely be necessary to focus restoration efforts on areas with the greatest likelihood of success. This may require some difficult decisions about which lands are most restorable. In ponderosa pine (*Pinus ponderosa*) forests, lower elevation ecotones seem to be at the highest risk for sustained invasions. The field site for this study was in lower elevation ponderosa pine forests, near the ecotone with pinyon-juniper (*Pinus edulis – Juniperus* sp.) woodlands. Similar low-elevation ponderosa pine forests have been invaded by cheatgrass (Fulé et al., 2005, Laughlin et al., 2005, Crawford et al., 2001). Conversely, several interior forest areas of northern Arizona have been resistant to invasion regardless of whether they were burned in wildfires or thinned and prescribe

burned in similar fashion to the treatments on Mt. Trumbull (Kuenzi et al., 2008, Stoddard et al., 2008, Moore et al., 2006, Huisinga et al., 2005). Furthermore, future climatic changes may alter plant community types, particularly at lower ecotones. Most climate change models predict that the lowest elevations of species distributions will be the most altered under future climate scenarios (Lenihan et al., 2003, Shafer et al., 2001). This suggests that disturbances to these regions will have greater uncertainty in successional trajectories of the post-disturbance plant community, with potentially greater risk of invasion by lower-elevation nonnative plant species. All these factors suggest that mid- and high-elevation areas of forest may have a better chance of successful restoration than the low elevation edges of the ecosystem (Laughlin and Fulé, 2008, Fulé and Laughlin, 2007).

Another factor important in triaging areas for restoration success is the presence of invasive nonnative plants, either within a managed landscape or in neighboring communities. This is another indicator of areas that at risk of invasion after disturbance. Whenever possible, areas containing nonnative species that are known to be highly invasive should be isolated from disturbance. While it is not always feasible, practitioners should consider creating buffers of unsuitable habitat between invaded areas and areas undergoing planned disturbances. Furthermore, severe disturbances to extant desirable vegetation should be minimized to reduce mortality and minimize the habitat made available for nonnative species to invade.

The timing of disturbances may also be manipulated to reduce the impacts of disturbances. At Mt. Trumbull, at the time of the initial restoration treatments, there was a sparse understory and heavy fuel loads when thinned plots were prescribed burned

(McGlone et al., 2009a,b). This may have led to a slower post-treatment response from the understory and allowed the initial establishment on cheatgrass across the project site. If promoting a robust native perennial grass understory is a desired outcome of the restoration project, then it might be advantageous to allow an extended rest period between the thinning and application of prescribed fire to allow the extant native community to increase. The benefits of a rest period after thinning have been supported by studies in northern Arizona that showed an increase in native understory production from thinning treatments with nonnative species than in thinned and burned treatments (Sabo et al. 2009, Moore et al., 2006).

Lastly, a multistage post-invasion remediation project could be enhanced by strategically timed treatments. Since cheatgrass is completely dependent on the seedbank for perpetuating the population, the timing of eradication treatments could be timed with both phenological stages of cheatgrass to maximize depletion of the seedbank. For example, herbicides such as Imazipac (Plateau™) work effectively on pre-emergent cheatgrass, but also adversely influence native species (Baker et al., 2009). Other herbicides have been shown to inhibit seed production in cheatgrass (Rinella et al., 2010). A light, strategically-timed application of herbicide, followed by plantings of native perennial grass plugs in the spring could help suppress cheatgrass and simultaneously promote native species.

This study highlights two important management concerns for cheatgrass-invaded systems. First, cheatgrass is successfully and persistently invading ponderosa pine forests of northern Arizona (Chapter 2). While cheatgrass has invaded many western ecosystems, ponderosa pine forests are rarely subjected to significant cheatgrass

invasions. Our results suggest that the risk of cheatgrass invasion into disturbed ponderosa pine forests is a serious concern, particularly at the lower elevational limits of the forests. Secondly, established native perennial grasses can out-compete cheatgrass (Chapter 4). The two species we used in our study, bottlebrush squirreltail and western wheatgrass (*Pascopyrum smithii*), as well as closely related species, have been shown to be strong competitors with cheatgrass in many ecosystems. The strong competitive ability of native perennial grasses could be utilized to mitigate the invasion potential of cheatgrass and other nonnative annual grasses.

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